THE COLOR VISION OF BIRDS

I. The Spectrum of the Domestic Fowl

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Evidence bearing upon the color vision of birds has come, thus far, chiefly from three sources; tests for the Purkinje phenomenon, discrimination tests with pigments, and photo-electric studies of the retina. Hess ('07) advanced the first evidence for the Purkinje phenomenon in birds. He placed white rice grains on a matt-black background, illuminated them with a spectrum, and placed fowls before them. The birds, light adapted, pecked first from the region of the orange through the red to the limit of the human spectrum, then in the yellow to blue-green, never in the blue or violet. Dark adapted and with a spectrum of low intensity they began to peck in the region of the yellow or orange-yellow and reached somewhat farther into the blue-green but never into the blue. Similar behavior was observed in the pigeon. The point of greatest stimulating value seemed to shift from the longer to the shorter wave-lengths with darkness adaptation. These results also led Hess to conclude that the spectrum of the day-bird is shortened at the violet end. In view of Watson's proof ('15) that the spectrum of the fowl is fully as extensive as that of man the validity of such a method as that of Hess becomes questionable.

Katz and Révész ('07 and '09) reported experiments with color-papers and stained rice grains in which fowls, when dark adapted and in dim light pecked more frequently at grains reflecting the shorter wave-lengths than when light adapted and

in bright light. A somewhat more conclusive test was made by Hess ('08) in measurements of the pupillary opening. The maximum contraction of the iris was produced by longer light waves in light adaptation than in darkness adaptation. A preliminary report of the writer's experiments was given by Watson ('14). They are recorded at length in the following pages. Yerkes ('15) using a similar method, obtained evidence of the change in the relative brightness values of the red and green with change of adaptation in the ring-dove.

Students of color discrimination in birds have usually employed color-papers or dyes with no certain control of intensity or saturation. Porter ('06) records tests with the English sparrow and cow-bird in which red, yellow, green, blue, and two shades of gray paper were used. The birds learned very readily to distinguish between these. Rouse ('06) used almost identical methods with the pigeon and secured like results. Katz and Révész ('07) trained chicks to pick out colored rice grains from among gray ones. As Hess ('12, p. 21) points out for the work of Katz and Révész, all these results might have been obtained with completely color blind animals. Hess ('12) reports tests with rice grains stained to match the Seebeck-Holmgren wools. Fowls distinguished the reddish grains from the greens and grays of this series, which were confused by a red-green blind man. From this Hess concludes that the fowl is sensitive to the wave-length of the red and green rays. The uncertainty of conclusions as to the color vision of animals drawn from analogy with the condition of brightness vision in color blind men has been pointed out by Frisch ('14) and the evidence of Hess himself for a shortening of the fowl's spectrum in the blue-green tends to invalidate his evidence for color vision. The careful work of DeVoss and Ganson ('15) shows in a practical way the justice of the most severe criticisms that have been urged against the use of color-papers in the study of animal vision.

Rouse ('05), by recording the rate of respiration in the pigeon after stimulation with light, was able to show an increase in rate progressive with change from the longer to the shorter wave-lengths. He was not able to find like changes with alteration in the intensity of light of constant wave-length. The tests with wave-length and intensity were not carried out under

like conditions, however, and the results obtained are not comparable. Katz and Révész ('09) advanced evidence for color fatigue in the fowl after exposure to red which seems to prove some differential action of wave-length. Yerkes ('15) showed the ability of the ring-dove to distinguish spectral red from green but did not control the brightness of the lights.

Finally the study of the action currents of the retina gives evidence of differential sensitivity to wave-length in day birds, Kohlrausch and Brossa ('14) obtaining characteristic types of galvanometer deflection for different wave-lengths irrespective of intensity. The correlation between action currents and color vision has not been made however.

All this evidence offers good ground for the presumption of a true color vision in day birds, yet the results are in no case absolutely conclusive. The question of the nature of the bird's spectrum, the number of primary colors, has not been approached experimentally. Hess describes the color vision of the fowl variously, as like that of a normal man, and as like that of a man looking through a piece of orange glass. He takes the latter view because of the supposed shortening of the spectrum at the violet end. Watson's data upon the threshold of the fowl make this view untenable. Beyond the probability that the bird is capable of some sort of reaction to wave-length, no definite conclusion can be drawn from the studies reviewed here. The details of spectral sensitivity, contrast, after images, color adaptation, and the rôle of color vision in the normal activities of birds are still open problems, promising to tax objective methods to the utmost.

The present paper offers further evidence for the existence of color vision in the fowl, in the form of data upon the relative stimulating effect of different wave-lengths upon the light and dark adapted eye, the ability of the fowl to react upon the basis of wave-length, and the appearance of relatively abrupt changes in the stimulating value of different parts of the spectrum. The experiments were begun in 1912, but, owing to delays incident to reorganizing the apparatus and to pressure of other work, they have progressed but slowly. The chief problem and the method of attack I owe to the suggestion of Professor J. B. Watson who has also given generously of his time in the readjustment and control of the apparatus. I am indebted,

likewise, to Dr. A. R. Middleton for assistance in equating the energies of the stimulus lights.

TECHNIQUE

Game Bantam cocks of somewhat impure breed have been used in all the tests, differential reaction to the stimuli being obtained by the Yerkes discrimination method with food, or food and punishment, as the stimulus to learning. Concerning the suitability of the fowls for experiments little more complimentary can be said than that they fit the apparatus. They show most of the peculiarities recorded by Yerkes for the dove and by Tugman for the sparrow, plus sexual reactions which sometimes make work impossible.

The Yerkes-Watson light apparatus, with some slight modifications for ease of manipulation, provided the visual stimuli. This apparatus gives two fairly pure monochromatic bands of which the wave-length, energy, and saturation are under accurate control (Yerkes and Watson, '11). These bands are reflected from similar plaster surfaces, 1 by 10 cm., exposed in the alleyways of the discrimination box. Three surfaces are used, one light being exposed constantly upon the middle surface, the other being shifted to the right or left in unison with lateral movements of the experiment box, thus effecting the interchange of the relative positions of the lights. This technique introduces a source of error which must be controlled carefully.

The primary distinction to be made in tests for color vision is between intensity and wave-length but reactions to other characters of the stimuli and experimental procedure must be guarded against. With the stimulus lights under complete control the discrimination method offers five other groups of stimuli which may lead to deceptive results. These are listed below together with the method of eliminating them in the final trials, in part as recommended by Yerkes and Watson (op. cit. p. 84 ff).

1. Cues from the movements of the experimenter.

a. The experimenter was probably never visible to the birds, certainly not in control experiments.

b. White lights were substituted for the monochromatic ones.

2. Cues from the noise and shifting position of the apparatus.

a. White lights as above.
b. Interchanging the monochromatic bands so that all movements of adjustment were reversed.
c. Pretense of shifts during training.

3. Unequal illumination of the passages due to the reflection of the shorter wave-lengths from black surfaces.

a. The apparatus was built to avoid this. (Yerkes and Watson l. c.)
b. White light was substituted alternately for each of the monochromatic bands.

4. Differences in the pattern of the stimulus plates.

a. Plates interchanged.
b. Lights interchanged.
c. White lights as above.

5. Light leakage in the apparatus and dark room.

a. Tests under 2 above.
b. The stimulus plates were illuminated directly by small Tungsten lamps, with and without interposed color filters.

These tests were all employed in the study of red-green discrimination and the more important also in all other tests except those upon the form of the spectrum. They gave always negative results: occasionally the chicks were detected in attempts to follow the movements of the experiment box, but they never learned to distinguish between a real shift in its position and the pretended shift which was made at every fourth or fifth trial. The results of the other controls limit the reactions definitely to the illumination of the stimulus plates in every important test. They will not be given in detail except where they bear upon brightness vision.

Adaptation was controlled in the following way. All tests were carried out in a completely darkened room with the experiment box enclosed in a black hood. When the chick made a correct choice a 4 ca. p. lamp 18 inches above the food dish was turned on until the chick picked up a bit of food, usually for less than one second. The chick was then returned to the starting box in darkness. Where light adaptation was desired, a 40-watt lamp with etched globe was held in the starting box for 30 seconds before each trial. That this produced a thorough brightness adaptation was shown by the following comparison

of the chick's time of reaction and the time required by the
experimenter to adapt to the stimulus lights, 1/45 of the standard
intensity. The experimenter's adaptation was always lighter
than that produced by looking directly at the 40-watt lamp
for 10 seconds.

Chick		Experimenter	
22 seconds		20 seconds	
14	"	16	"
4	"	6	"
18	"	10	"
6	"	4	"
14	"	20	"
2	"	3	"
6	"	2	"
3	"	3	"

When darkness adaptation was desired the chick was exposed
to light for only the moment when he pecked at the food. Be-
fore the experiments he was kept in the dark for one hour, this
being the time required for complete darkness adaptation
(Hess '07).

THE PURKINJE PHENOMENON

Experiments were begun with two Bantam cocks, A and C.
They were first tested with white light and were found to be
markedly photopositive, invariably going to an illuminated
plaster surface. Two white lights of different intensity were
then introduced. The chicks showed a tendency to choose the
brighter of the lights but their discrimination was very inaccurate
and when the dimmer of the lights was well above their threshold
they no longer selected the brighter: the reaction was evidently
to the light as an object. An attempt was then made to increase
the accuracy of their discrimination. Food was given at the
brighter light and no food at the other. Training under these
conditions was continued from October 23 until January 31
with ten trials per day.

During this time it was found impossible to get the chicks
to distinguish accurately between white lights of relative in-
tensities less than ten to one (absolute intensities of 18 and
1.8 ca. m.). They showed a slight preference for the brighter
of two lights of intensities three to one (18.0 and 6.0 ca. m.)
but never made ten successive reactions without error. I
believe that the ratio of three to one represents very nearly
the difference limen of the fowl under the conditions of these
experiments. It is possible, however, that with a stronger

motive than hunger the apparent limen might be much lessened. The statements of other investigators imply that the chick is very strongly photo-positive and will choose the brighter of two lights of almost equal intensity. As this was found to be untrue, long training in brightness discrimination was necessary in order to prepare the animals for the following experiments upon the Purkinje phenomenon. The training was continued for 500 trials after fairly accurate brightness discrimination had been established. Many changes in the brightness of the lights, position of the experiment box, noise of rotating sectors, illumination of the experiment box, etc. were introduced to accustom the animals to changing experimental conditions.

When reactions to brightness had become automatic monochromatic lights were substituted for the white lights. Those first introduced were Red 650$\mu\mu$ and Green 520$\mu\mu$. The intensities of the two beams were equated with each other by the method and with the standard of Pfund[1] ('12, Yerkes and Watson, '11).

a. The fowls, light adapted, were offered a choice of the stimulus plates with these lights at standard intensity, food being given at every trial. They chose—

	Green	Red
Chick A..............	12	9
Chick C..............	19	11
Average............	63%	37%

The green had perhaps the greater stimulating value under these conditions but the difference in brightness for the chick was evidently not very great.

b. The chicks were next dark adapted for one hour and the illumination of the stimulus plates was cut down to 1/90 of the standard intensity. Chick C was tested under these conditions. He chose—

Green	Red
13	1
93%	7%

At this energy the green had a much greater stimulating value.

[1] This standard has not been expressed in other terms. The stimulus patches illuminated at the standard energy have a luminosity which I estimate for 580 $u\mu$. at 2 candles per square meter. In the tests for the Purkinje phenomenon the lights were equated with the Pfund standard after reflection from the stimulus patches. In all other tests the energies of the beams were equated before reflection from the diffusing surface.

Control experiments indicated that the red was below the chick's threshold and that he was reacting to it as to darkness. The intensity of the lights was next increased to 1/45 of the standard and Chick A was offered a choice of them. He chose—

Green	Red
9	1
90%	10%

Furthermore, when offered a choice between the red and darkness he chose the red in 8 of 10 trials showing that the red was above his threshold. At low intensities the green has a much greater stimulating value than the red for the dark adapted chick.

c. With the energies of the beams at 1/90 standard, Chick A. light adapted, was introduced into the discrimination box. He chose—

Green	Red
10	0
100%	0%

As a control he was offered a choice between the red and darkness. He chose the red in 10 consecutive trials. The red used was below the threshold of the experimenter when light adapted and a record of the time of adaptation of the experimenter and the time of reaction of the chick shows that the chick also required a slight darkness adaptation before the red became visible to him. His accurate choice of the green at this energy was undoubtedly due to the fact that the choice was made before the red came above threshold.

d. The energies of the beams were increased to 1/9 of the standard. Chick A, dark adapted for one hour, chose—

Green	Red
5	5
50%	50%

The energies were immediately reduced to 1/18 and he chose—

Green	Red
3	3
50%	50%

Under the same conditions Chick C chose—

Green	Red
4	6
40%	60%

When the energy is as great as 1/18 of the Pfund standard

the greater stimulating value of the green is lost, irrespective of the degree of adaptation.

The results are thus far valuable only as illustrating sources of error in tests for the Purkinje phenomenon. In tests a and d no evidence for a greater stimulating effect of either light was obtained; in b and c the results are due, in all probability, to the reduction of the intensity of the red to threshold value and not to the process of adaptation. It seems probable that two factors may produce spurious evidence of the Purkinje phenomenon in experiments with animals. 1: While two lights of unequal energy may not produce a reaction upon the basis of brightness at high intensity, a reduction of their intensity may bring the weaker below threshold while the other is still visible. From data obtained during training with white lights it is clear that when two lights differing greatly in stimulating value are exposed together the reaction to the less intense may be lost while it still persists when this stimulus is exposed alone or with another of equal stimulating value. In work of this sort it seems necessary, then, to distinguish two types of threshold; a lower threshold determined by the absolute sensitivity of the eye, and a higher one, which might be termed the threshold of attention, due to the interference of the stimuli. 2: With lights of unequal intensity differing in brightness at high intensity by less than the limen of the animal the action of the Weber-Fechner law might produce a perceptible difference following a reduction of the intensity of the lights.

These factors, in all probability, would have produced the results obtained in all the recorded tests for the Purkinje phenomenon if a band of white light of properly graded intensity had been used instead of the spectrum. I am inclined to think that the methods of Hess, Katz and Révész, Yerkes, and my own recorded above are too crude to give a proof of the Purkinje effect and that the results obtained are due rather to one or other of these secondary phenomena. The records of the Purkinje effect in man are so conflicting that an analogy between man and other animals seems hardly profitable. The resemblance in the distribution of cones of the day bird's retina to the human fovea, where probably the phenomenon does not appear (Nagel '11), is sufficient, however, to demand extreme caution in interpreting results in this field.

With the uncertainty of the discrimination method it seems necessary either to introduce some technique which will eliminate fluctuations of attention or to test for the relative stimulating effects of monochromatic lights when the energy remains constant and only the state of adaptation changes. In testing for the Purkinje phenomenon I did not realize the necessity for avoiding threshold stimuli and so carried out only a few tests with constant light energies.

Contrary to the statements of Hess the red never seemed to have a greater stimulating value than the green of equal energy either for the light or for the dark adapted chick. (The energy of the red which he used was probably much greater than that of the green.) By a series of tests an energy relation was determined at which the red was just brighter than the green for the light adapted chick. This was at red 1/6, green 1/45 of the standard. When the energy of the red was decreased to 1/18 there was no choice, when it was increased to 2/9 it was chosen accurately and without hesitation. With red 650 $\mu\mu$, intensity 1/6, and green 520 $\mu\mu$, intensity 1/45, Chick C, light adapted, chose—

Red	Green
11	2
84%	16%

He was dark adapted for one hour, then chose—

Red	Green
4	6
40%	60%

Light adapted immediately he chose—

Red	Green
3	1

Chick A under the same condition became erratic, developed a position habit, and gave no results that can be interpreted. The few records of Chick C indicate that there is a shift in the point of greatest stimulating value of the spectrum from the longer to the shorter wave-lengths with increasing darkness adaptation. The number of trials is too small for certainty.

As there was the danger of association of one or other color with food work with red and green was dropped at this point and the apparatus was arranged to give yellow 590 $\mu\mu$. and blue-green 500 $\mu\mu$. at equal energies. Both lights were cut

down to 1/90 of the standard; at this energy both are above the chick's light adapted threshold. Chick A, fully light adapted was placed in the experiment box. He chose—

Green	Yellow
7	7

Chick C was dark adapted for one hour, then offered the lights. He chose—

Green	Yellow
7	5

Light adapted immediately afterward, he chose—

Green	Yellow
4	5

At this intensity neither of the colors has a markedly greater stimulating value than the other. At the same energy the red drops below the light adapted threshold.

A point was determined at which the yellow was just brighter than the green for the light adapted chick. This was yellow 4/90, green 1/90. Light adapted, Chick A chose—

Green	Yellow
3	21

After dark adaptation he chose–

Green	Yellow
4	2

Chick C was tested in the same way but for some unexplained reason showed a complete breaking down of his reactions; even failing to choose between light and darkness. This lasted for several days and Chick A also became erratic so that the tests could not be continued without retraining for brightness. Such experiments, with food at every trial, make heavy demands upon the retention of earlier habits and it is surprising that the reaction persisted as well as it did. The apparent shift in brightness for the yellow and green, like the last test recorded for the red and green, indicates a Purkinje effect of adaptation.

The determination of energies of the monochromatic lights having equal brightness values for the chick (the brightness equation point) is of interest when compared with the respective thresholds for the same wave-lengths and is of primary importance for tests for color discrimination. The values that I

have determined are very rough but they indicate that the relative stimulating value for the light adapted eye of monochromatic bands of high intensity is proportional to the threshold values of the same wave-lengths with light adaptation, as determined by Watson ('15).

SENSITIVITY TO WAVE-LENGTH

As the primary object of these experiments was to determine whether or not the chick is sensitive to differences of wavelength and as six months had been consumed already in the preliminary tests it was thought best to abandon the latter and test for color discrimination. Red 650 $\mu\mu$. and green 520 $\mu\mu$. at equal energies were used as stimuli. Preference tests were of course impossible with chicks A and C.[2] Learning was rapid and after 200 trials the chicks were judged ready for control tests. The control tests described on page 5 limited the reaction to the illumination of the stimulus plates. Tests to distinguish between reaction to energy and to wave-length were made by altering the brightness relations of the saturated lights, and by diluting them. As determined in the Purkinje tests the brightness equation point for 650 $\mu\mu$. and 520 $\mu\mu$ is somewhere near the energy relations of 8 to 1. The energy relation of the stimulus lights was varied in both directions from this ratio as described in table 1. Tests with the colors diluted were made as indicated in table 2. The results of these tests, summarized in table 3, show that a reversal of the brightness values of the red and green did not seriously disturb the accuracy of the discrimination. The errors made appeared when the energy of the positive light was much reduced, irrespective of whether this was red or green. The dilution tests give fairly clear evidence of discrimination except in the case of Chick C with dilute red.

[2] The behavior of some other birds in tests for color preference seems worth recording. Training for red-green was begun with five hens but not completed. Four of these showed no color preference for the lights at the brightness equation point for light adaptation. The fifth under the same conditions chose the green in preference to the red in 20 successive trials. This behavior suggests either an acquired color preference or color-blindness. Unfortunately, this bird was killed by rats before her vision could be tested.

TABLE 1

Tests for red-green discrimination with varied brightness relations of the stimulus lights. The energies at which the red was known to be brighter are printed in italics. In the remaining tests the brightness value of the green was equal to or greater than that of the red. Energies are expressed in decimals of the Pfund standard.

Chick A (*Positive to red*)				Chick C (*Positive to green*)			
Energies		No. of trials	No. of errors	Energies		No. of trials	No. of errors
Red	Green			Red	Green		
1.0	1.0	5	1	1.0	1.0	5	0
1.0	*.022*	5	0	*1.0*	*.022*	10	2
1.0	*.044*	5	0	*1.0*	*.044*	5	0
1.0	*.088*	5	0	*1.0*	*.088*	10	3
1.0	.177	5	0	1.0	.177	5	0
1.0	.355	5	0	1.0	.355	5	0
1.0	.500	5	0	1.0	.500	5	0
1.0	1.0	5	0	1.0	1.0	5	0
.022	1.0	9	3	.044	1.0	10	0
1.0	*.022*	6	0	*1.0*	*.022*	10	3
.022	1.0	10	3	.022	1.0	10	2
.088	1.0	10	0				

TABLE 2

TESTS FOR RED-GREEN DISCRIMINATION WITH VARIED SATURATION
OF THE STIMULUS LIGHTS

Condition of stimuli	Chick A		Chick C	
	No. of trials	No. of errors	No. of trials	No. of errors
Both lights at standard energy............	5	0	5	0
Green much diluted......................	10	1	6	0
Bright white light substituted for green.....	5	3	5	1
Both lights at standard energy.............	10	0	5	1
Red much diluted........................	10	0	10	4
Red diluted until its quality was lost........	7	4	..	..
Both lights at standard energy.............	5	0	5	0
White light of low intensity for red.........	8	0	12	4
Same white for green.....................	10	1	6	0
White light of high intensity for red........	5	0	6	3
Same white for green.....................	10	3	5	0
Both lights at standard energy.............	5	0	6	0
Two white lights of equal brightness........	10	5	10	2*

* A careful examination was made for secondary criteria which might account for this choice which tends to invalidate all the results obtained with Chick C. Nothing could be discovered by the dark adapted human eye. The test was repeated on the following day, when ten trials with five errors were obtained. The above record was probably a chance variation.

TABLE 3

SUMMARY OF FIRST TESTS FOR RED-GREEN DISCRIMINATION

Condition of stimuli	Chick A (*Positive to red*)		Chick C (*Positive to green*)	
	No. of trials	No. of errors	No. of trials	No. of errors
Red 1: Green 1.......................	35	1	31	1
Red below 0.1: Green 1...............	29	6	20	3
(green brighter)				
Red 1: Green below 0.1...............	16	0	20	5
(red brighter)				
Green dilute: Red 1....................	10	1	6	0
Red dilute: Green 1...................	10	0	10	4
Red greatly diluted: Green 1..........	7	4	..	.
White light for red....................	13	0	18	7
White light for green..................	25	7	16	1
Controls				
White light of equal energy............	20	13	20	7
Red 1: Darkness.....................	5	To D. 0	15	To D. 5
Green 1: Darkness...................	10	To D. 4	10	To D. 1

The tests in which white light was substituted for each of the lights in turn are interesting as indicating the relative importance of the negative and positive stimuli in determining the reaction. Both chicks confused the white with the positive stimulus (table 3) and distinguished it readily from the negative. Punishment had been used in this case with the negative light which here appears to be most clearly recognized. In later experiments without punishment conditions appear to be reversed, the negative light being most frequently confused with the white. This is in accord with the view that punishment is the more efficient factor in learning. The tests also evidence either color discrimination or accurate perception of brightness. The use of the lights singly gives further evidence of the same sort, since darkness was chosen fewer times with the positive color than with the negative (table 3).

The work had to be dropped at this point. The tests recorded make it highly probable that the birds were reacting upon the basis of wave-length, but as the energies of both red and green were never altered simultaneously, the possibility that an extremely accurate perception of absolute brightness furnished the basis for reaction was not completely eliminated. It seemed

advisable therefore to repeat the experiment using still more thorough controls.

After a long delay, while smoked wedges were substituted for the Aubert diaphragms used in equating light energies, the work was resumed. Three cocks, A (now three years old), and two younger ones, D and E, were trained for discrimination with red 650 $\mu\mu$. and green 520 $\mu\mu$. uncalibrated, just as given by the carbon arc spectrum. Chick D was trained to avoid the red (middle stimulus plate) and choose the green; Chicks A and E to choose the red. After about 400 trials the chicks began to react perfectly. They were given an additional hundred trials to make the reaction more nearly automatic—then, as the lights could not be equated immediately, a series of rough control tests for brightness and secondary criteria was begun, partly to accustom the chicks to a changing problem and partly as a test of their sensitivity to wave-length. Three types of tests were employed to distinguish between brightness and wave-length; 1, first one, then the other light was reduced to threshold intensity while the other remained at the full energy of the spectrum; 2, a white light of constant intensity was substituted for each of the colored lights in turn; 3, each light was exposed alone with one passage completely dark. Table 4 shows the records of the chicks in the first of these tests. It will be noted in the results of this experiment that reduction of the intensity of the negative color produced no disturbance of the reaction while reaction of the positive color led to many errors. Had the reaction been due to the relative brightness of the stimulus patches Chick D should have been disturbed when the red was reduced, as were A and E, since this must then have represented the condition in which the difference in brightness approached threshold. Instead of this, however, Chick D reacted inaccurately only under conditions where A and E remained undisturbed. This seems to limit the effective stimulus either to the wave-length or to the absolute intensity of the positive stimulus patch.

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TABLE 4

REACTIONS TO RED AND GREEN LIGHTS OF ESTIMATED THRESHOLD VALUE

	Intensity of lights		Chose	
	Red	Green	R.	G.
Chick A.	Just above threshold	Full intensity	47	18
(*Positive to red*)	Well above threshold	Full intensity	20	0
	Full intensity	Just above threshold	10	0
Chick E.	Just above threshold	Full intensity	35	10
(*Positive to red*)	Well above threshold	Full intensity	14	1
	Full intensity	Just above threshold	15	0
Chick D.	Just above threshold	Full intensity	0	9
(*Positive to green*)	Full intensity	Just above threshold	23	12

The second group of tests, made with Chicks D and E gives additional evidence against a reaction to the relative brightness of the stimulus patches. A very intense white light (the image of a Nernst glower directed upon the stimulus patch by a 2-inch lens of 6-inch focus) was first substituted for the red light, the green light being left at full intensity somewhat diluted by light reflected from the white stimulus patch. Under these conditions Chick E (*positive to red*) chose—

White	Green
11	1

Chick D (*positive to green*) chose—

White	Green
3	13

The white was then substituted for the green and the red was restored at full energy. The records of the birds were—

	White	Red
Chick E............	1	9
Chick D............	4	1

The intensity of the white light was many times that of the monochromatic so that the brightness relations of the stimulus patches were certainly reversed in the two tests. The probability of reaction to absolute brightness is also reduced by the dilution of the monochromatic lights by light reflected from the white patch. For me this reflected light had greater brightness than either of the monochromatic lights.

To avoid a reaction to secondary criteria given by the shifting

of the lights and experiment box the monochromatic lights were
arranged so that both could be projected upon the same stim-
ulus patch. They were exposed in irregular order with the
other patch illuminated with the intense white light. Under
these conditions Chick E chose—

Red	6	White 6	when r and w were exposed together.
Green	1	White 5	when g and w were exposed together.

Chick D chose—

Red	2	White	4
Green	5	White	0 under the same conditions.

The white light was immediately reduced to threshold intensity
and the tests repeated.
Chick E chose—

Red	8	White 1
Green	3	White 8

Chick D chose—

Red	2	White 5
Green	5	White 0

The change in the intensity of the white light with the resultant
change in the dilution of the monochromatic points to a sen-
sitivity to wave-length. The complete change in the technique
eliminates a reaction to secondary criteria.

The conclusions from the third set of tests are based upon
the time of reaction to a single monochromatic light: the time
required for the chick to go from the door of the starting box
to the food dish, a distance of 3 feet. The results of the tests
with the three chicks are given in table 5. During these tests
the intensity of the lights was varied from 1/18 to the full energy
of the spectrum. The birds, although instinctively photo-
positive, showed a marked delay in advancing to the negative
light, irrespective of its intensity. Unless the brightness differ-
ences of the monochromatic lights for the chicks are extremely
great this experiment is sufficient to eliminate reaction to the
absolute intensity of the light.

These tests are given in some detail as illustrating a fairly
satisfactory technique when the energy and brightness values
of the stimulus lights are unknown. Such methods have the
disadvantage of introducing many disturbing elements; in such
tests the animals ultimately become confused and give con-
flicting results.

TABLE 5

Time of reaction to one light alone. The time is that required by the chicks to go from the door of the starting box to the food dish, a distance of three feet.

Red light alone at varied intensity	No. of trials	Average time	No. of errors (Darkness chosen)
Chick A. (*Positive to red*)............	8	1.45 sec.	0
Chick E. (*Positive to red*)............	12	2.12 sec.	0
Chick D. (*Positive to green*)..........	5	30.60 sec.	4
Green light alone at varied intensity			
Chick A.......................	8	7.25 sec.	3
(Refused to advance in three trials)			
Chick E.......................	8	16.37 sec.	2
Chick D.......................	14	5.60 sec.	0

At the end of these tests the lights were equated in energy, the chicks were retrained for a few days to increase the accuracy of their reactions and then tested with the lights under accurate control. The energies of the lights were varied widely in both directions from the brightness equation point and were likewise varied in absolute intensity at different brightness ratios. The results of the tests with the three chicks are given in table 6. At the end of the experiments the chicks were offered two white

TABLE 6

Tests for red-green discrimination with varied brightness relations of the stimulating lights. Arranged as table 1.

Chick A. (*Positive to red*)				Chick E. (*Positive to red*)				Chick D. (*Positive to green*)			
Energies		No. of trials	No. of errors	Energies		No. of trials	No. of errors	Energies		No. of trials	No. of errors
R	G			R	G			R	G		
2.0	1.0	15	1	2.0	1.0	20	0	2.0	1.0	20	1
1.0	1.0	68	8	1.0	1.0	20	4	1.0	1.0	20	1
1.0	.5	10	0	.5	1.0	5	0	.5	1.0	10	1
1.0	.25	10	0	.5	.11	10	0	*2.0*	*.11*	12	1
1.0	*.10*	10	1	.25	.5	10	1	Injured by Chick E.			
1.0	*.05*	10	0	.25	.11	20	2				
2.0	*.05*	10	1	.11	1.0	15	0				
2.0	*.08*	5	0	.11	.11	9	1				
2.0	.15	10	0	*2.0*	*.11*	15	0				
.44	1.0	15	0	*2.0*	*.08*	10	0				
.22	1.0	20	2								
.22	.22	10	1								

lights of equal intensity exposed under the same conditions
as the monochromatic. Chick A chose the stimulus patch to
which he usually reacted positively 7 times, the other 8 times.
Chick E chose the central patch 6 times, the other 4. Chick
D could not be tested. A was further offered a choice of two
white lights of relative intensities 1 to 90. He chose the brighter
7 times, the other 3; an accuracy less than that with any in-
tensity of monochromatic lights. These tests, with the other
controls mentioned in the discussion of technique limit the
efficient stimulus to the illumination of the stimulus plates.
Summarizing table 6 we find that with the red certainly brighter
than the green the chicks made 3 errors in 72 trials or 4.1 per
cent. error. In 325 trials with the green brighter or equal to
the red in brightness they made 23 errors or 7.7 per cent.
Further, in trials where the intensity of both lights was greatly
altered there was no reduction in the accuracy of choice, so
that the possibility of reaction to the absolute brightness of
either stimulus is eliminated. As between brightness and wave-
length, then, these experiments speak conclusively for the latter.
The possibility of other characters of the stimulus lights them-
selves furnishing the basis of discrimination will be considered
after the work with yellow and blue light has been recorded
(page 20).

The same three fowls were trained with yellow at 588 $\mu\mu$.
and blue-green at 500 $\mu\mu$. with energies equal. Chicks A and
E were trained to choose yellow, D to choose green in order
to take advantage of the previous training. Strangely enough
the chicks were confused by the green at 500 $\mu\mu$, not greatly
different from 520 $\mu\mu$. to my eyes, and failed to discriminate
in the first trials. They had previously reacted to 520 $\mu\mu$ when
white light, darkness, or yellow were substituted for the red.
However, after 120 trials they gave less than ten per cent. error
and were considered ready for control tests. Tests for the
Purkinje effect had previously shown that the following bright-
ness values held for these wave-lengths for the moderately light
adapted eye of the fowl.

Yellow	Green	
4	1	yellow brighter.
2	1	yellow perhaps brighter.
1	1	neither brighter.
1	45	green *certainly* brighter.

Tests at these values were carried out with the results shown in table 7. The ratio of 45 to 1 gives uncertain results owing

TABLE 7

Tests for yellow-green vision with varied brightness relations of the stimulus lights. Figures in italics show where the yellow is brighter for the chick.

Energies		Chick A.		Chick D.	
Yellow	Green	Trials	Errors	Trials	Errors
1.0	1.0	14	2	20	4
.01	1.0	20	2	20	2
.11	2.2	14	1		
.05	1.0			10	0
2.0	*1.0*	29	6	12	1
1.0	1.0			10	1

to difficulty with the apparatus: a reduction of the yellow below .1 of the standard brings it near the chick's threshold[a] and a greater energy of the green than 2.2 could not be obtained with the present arrangement. The tests are therefore not as extensive as I desired. However, chicks long trained to brightness discrimination failed to distinguish this red and green even at the energies of 1 to 1 and the tests with variations in both directions from this ratio seem adequate to eliminate a reaction to brightness. As in the case of red and green the effective stimulus is restricted to wave-length.

The evidence for color vision thus far presented seems to prove that the chick can distinguish between monochromatic lights of any intensity between threshold and the Pfund standard, irrespective of the brightness or saturation. The effective stimulus is the wave-length. The question remains, is the discrimination based upon retinal sensitivity to differences of wave-length or upon some entoptic phenomenon.

The difference in visual acuity in light of different wave-length is well known, and, though it seems to be largely a matter of relative brightness it may furnish a basis for discrimination. Whether a like variation in acuity occurs in the color blind I cannot discover from the literature. Allied to this phenomenon is that of diffraction or dispersion within the eye. At low intensities the red and yellow stimulus patches have for me sharp outlines while the green of equal brightness lacks sharpness

[a] The absolute intensities of the lights in this experiment are not comparable with those of the Purkinje tests. The introduction of the smoked wedges cut down the energy of the spectrum so that the equation of the lights with the Pfund standard had to be made before they were reflected from the plaster surfaces instead of afterward as in the first experiment.

and seems to be surrounded by a luminous halo. It seemed possible that the birds were reacting upon the basis of the sharpness of the visual objects rather than upon their color, either as a result of diffraction or of serious chromatic aberration.

Tests were made at different times during the experiments with a view to controling these factors and gave the following results.

1. Wide variations in the size and shape of the stimulus plates were without effect.

2. High intensities and dilutions, reducing the apparent diffraction of the shorter wave-lengths and giving sharp outlines for me to both stimulus plates did not effect the reaction of the birds.

3. Intense white light with imperfect color filters, completely altering the secondary phenomena for me, were discriminated as promptly as the spectral lights.

4. The evidence given in the following section for abrupt changes in the reaction value of the spectrum is difficult to explain by these phenomena.

The visual acuity of the fowl determined by Johnson ('14) seems to eliminate the question of any great chromatic aberration in the chick, and the foregoing tests make a reaction upon any other basis than retinal sensitivity highly improbable.

THE CHARACTER OF THE SPECTRUM

With the establishment of sensitivity to differences of wave-length the problem of the difference limen for wave-length in different parts of the spectrum at once suggests itself. A thorough solution of this problem would require months of training with careful controls of brightness at every stage. The Yerkes-Watson apparatus is not well adapted for such experiments as it cannot be arranged readily to give lights from adjacent parts of the spectrum. The following tests, serve to give a clue to the form of the spectrum of the bird, particularly with reference to the existence of regions of widely different reaction value separated by relatively short intervals of the spectrum.

Chick A, positive to 650 $\mu\mu$. and negative to 520 $\mu\mu$. was offered red 650 and yellow 580 $\mu\mu$. He chose the red six times in seven trials and showed little confusion. The red was evi-

dently different in reaction value from the yellow. The element of intensity was not eliminated here but since the chicks had been reacting so well to wave-length and not at all to brightness differences I think it unlikely that the discrimination was made here or in the following tests upon the basis of brightness.

Chick E, trained like Chick A, was given 7 trials with 650 $\mu\mu$. and 520 $\mu\mu$, making no error. The red was then shifted toward the shorter wave-lengths with the following results.

Wave-length, $\mu\mu$.		Chose		
"Red"	Green	"Red"	Green	Character of longer waves for the human eye
650	520	7	0	Red.
610	520	5	0	Red-orange.
600	520	6	0	Orange-yellow.
580	520	3	3	Yellow. Position habit.
590	520	3	0	Yellow-orange. Secondary evidence of discrimination.

This indicates that there is a change in the reaction value of the spectrum between 580 and 590 $\mu\mu$. This is the region in which the yellow assumes an orange quality for man.

Chick D, positive to green, was first given 5 trials with the red and green as in training, making no error. The test was continued as follows:

Wave-length, $\mu\mu$		Chose		
Red	"Green"	Red	"Green"	
650	520	0	5	
650	600	0	5	Reactions prompt.
650	630		Position habit developed at once.	

This indicates a change in the reaction value of the spectrum between 600 and 630 $\mu\mu$. This is the region of the transition from red to orange for man.

Chick A was given the following tests.

Wave-length, $\mu\mu$.		Chose	
"Red"	Green	"Red"	Green
650	520	5	0
610-590	520	5	0
590-565	520	5	1

(The reaction here with green and yellow was given upon the basis of the green as negative color, the chick going to darkness in preference to green.)

550-530	520	2	2 Refused to advance.

This suggests a change in the character of the light between 530 and 565 $\mu\mu$, corresponding roughly to the change from yellow to green for man.

After training with yellow and blue-green Chick D was given the following tests.

Wave-length, $\mu\mu$.		Chose	
"Yellow"	Green	"Yellow"	Green
580	500	1	6
535	500	Right position habit.	
565	500	0	5
565	500	0	3

(1/18 standard)

There is a change between 535 and 565 $\mu\mu$. This agrees with the results obtained from A. The change in the energy of the yellow was made as a slight control of the brightness element.

Chick A was offered green 530, violet 460 $\overline{\mu\mu}$. The use of the yellow-green was due to the difficulty of obtaining lights nearer together in the spectrum. In an earlier experiment after training with red and green Chick A had been offered a choice between white and red, white and blue, and red and blue (impure color filters). He chose accurately red and blue in preference to white, red in preference to blue and all in preference to green 500 $\mu\mu$. I expected him to choose the violet in preference to the green and refused him food at the latter. Instead, however, he chose the green five times in succession, then, getting no food, developed a position habit. He was then fed at the green and immediately chose it five times in quick succession.

Chick D was offered a choice between 500 and 460 $\mu\mu$. He showed no choice and developed a position habit immediately.

It is rather difficult to interpret the results of these two tests with the assumption of identical color divisions for the chick and man. In the beginning of training with yellow and blue the shift from 520 to 500 $\overline{\mu\mu}$. seemed to confuse the chicks (page 19). If we suppose that there is a marked change in the reaction value of the spectrum between these wave-lengths, there seems to be a general agreement in the results; for Chick A 530 $\mu\mu$ and 580 $\mu\mu$. resembled each other more than they did 500 $\mu\mu$, and 460 $\mu\mu$ perhaps resembled 500 $\mu\mu$; for Chick D 500 $\mu\mu$ and 460 $\mu\mu$ were more nearly alike than the original 580 $\mu\mu$ and 500 $\mu\mu$. The accord of the animal's behavior with this interpretation justifies the assumption, pending more accu-

rate investigation, that there is a marked change in the reaction value of the spectrum between 500 and 530 $\mu\mu$ with no marked change between 500 and 460 $\mu\mu$, i. e., the region corresponding to the blue and violet for man begins at a longer wavelength for the chick.

To summarize this part of the work, the accuracy of the discrimination of the fowls is affected by changes in the position of the stimulus lights through the following intervals and it is suggested that the wave-lengths lying between each pair of these intervals, which are probably shorter than the tests indicate have a fairly uniform reaction value.

$$\begin{array}{l} 630 - 600 \; \mu\mu. \\ 590 - 580 \; " \\ \{ \; 565 - 550 \; " \\ \} \; 565 - 535 \; " \\ \{ \; 520 - 500 \; " \\ \} \; 540 - 470 \; " \end{array}$$

THE RELATIVE REACTION VALUE OF INTENSITY AND WAVE-LENGTH

In field studies of animals where the conditions of illumination are not under control it is difficult to determine whether the animal, even if known to have color vision, is reacting to color or to brightness. The distinction is of importance in many biological problems where the necessity for natural conditions makes an actual test of the efficient stimulus impossible. The only clue to it in such cases is given by the relative ease with which habits of reaction to the two attributes of the light stimulus are formed. The data upon the rate of learning in my experiments gives some indication of the relative efficiency of wave-length and intensity in light stimuli.

a. Birds already trained in brightness discrimination, when trained with red and green of different brightness values for them (red 650, green 520 $\mu\mu$. at equal energies) changed quickly to reaction upon the basis of wave-length, *without any alteration in the brightness values of the lights which might have destroyed the habit of reacting to brightness.* After training with colors the association with wave-length was dominant even when the brightness values of the stimuli were so greatly different as to call out the instinctive brightness preference in untrained birds.

b. The conditions under which training for brightness and color discrimination have been carried out are not strictly

comparable, but some unrecorded experiments by Dr. Middleton and myself upon the fowl's difference limen for brightness indicate that where threshold intensities are not involved habits of reaction to brightness are established with much greater difficulty than are those of reaction to wave-length.

From the evidence even of a. alone I believe that the field experimenter may feel confident that, if the birds show a differential reaction to colored objects not differing enormously in brightness for him, their reactions are made upon the basis of wave-length.

DISCUSSION

One fact the experiments seem to have brought out clearly: The fowl is sensitive to differences of wave-length irrespective of intensity and its sensitivity is greater than, or at least different from, that of any form of partial color blindness in man. Less certainly it appears that for the fowl the spectrum is divided into areas of widely different reaction value, of which there are not less than five, probably more. It is not probable that all these occupy areas of the spectrum corresponding to the more conspicuous divisions for man. There is also some slight evidence for a Purkinje effect but this needs verification.

The proof of color vision in the fowl should make possible the more ready correlation of the so-called physiological methods of studying sensitivity with other behavior methods. The probability that the specific action-currents of the retina following stimulation with different wave-lengths are an index to a more general color sensitivity is increased. The lack of such specific action-currents in night birds furnishes a final test of the interpretation of retinal action currents. Experiments upon the color vision of owls are in progress. The value of such methods as those of Rouse and Bàbàk is also enhanced by a verification of some of their results by other methods. The reflex responses offer an index of sensitivity more accurate and convenient than the discrimination method, but they must be correlated with other activities of the animal before they can furnish a basis for attack upon more general problems.

The probability of a high degree of sensitivity to wave-length in other day birds suggests anew the problems of organic and sexual selection in birds, problems which have largely fallen into disrepute of late. The prominent rôle played by sensitivity

to wave-length as compared to brightness offers the possibility of field and experimental studies of these much discussed questions where the experimenter may feel reasonably confident that his results are due to color perception.

The conclusion of Katz and Révész that the Purkinje phenomenon cannot be explained by the process of adaptation in the rods does not seem to be justified since neither the Purkinje phenomenon nor the absence of visual purple has been established for birds. It seems too early yet for a satisfactory correlation of structure and function. Further studies of adaptation upon birds with different retinal composition will doubtless help to clear up the question of the function of the retinal elements.

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THE BIOLOGY OF THE MUD-DAUBING WASPS AS REVEALED BY THE CONTENTS OF THEIR NESTS

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With five plates

This paper is primarily a study of the contents of the nests of three species of mud-daubing wasps. Before entering upon a discussion of how the nests are provisioned and how the young fare in their struggle against adversities and enemies, it will be well to become familiar with the nests themselves, their structure, their sites, decorations, etc.

Fossorial Hymenoptera are roughly classified, according to their habits, in four groups: 1. Those which build no special receptacles for their young but are either parasitic or subparasitic, or take advantage of the abodes of other insects, holes, etc.; 2. Builders of cells in the form of pottery constructed of clay mixed with water or saliva and dried; 3. Excavators of burrows in the ground; 4. Makers of tunnels in wood or the stems of plants.[1]

The three species of Fossorial wasps herein dealt with belong to the second group of this classification, those wasps which construct cells of clay or mud as receptacles for their young and its provisions. The mothers themselves do not use these structures for their own shelter, but go elsewhere for the night. All three of these species are spider ravagers.

First we have the pipe-organ type of mud nests (see figs. 1, 2, 5) built by *Trypoxylon albitarsis* Fab., the shiny black wasp with beautiful white toe-tips. Then we have the familiar mud nests which at first sight look like a clod of earth; these are made by two species belonging to the subfamily Sceliphroninae, *Sceliphron (Pelopoeus) caementarium* Drury, a pretty black wasp trimmed up in yellow (this wasp is commonly known by the boys in my neighborhood as "yellow-legs"), and the beautiful steel-blue wasp, *Chalybion caeruleum* Linné. The nests of these

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[1] Sharp, D. Insects, Pt. II. *Cambridge Nat. Hist.*, p. 90.

two species are so similar as to be indistinguishable (figs. 3, 4, 6, 18).

Some authors have placed these two wasps in the same genus, probably chiefly because of their similar habits of nesting, but I have found that there is some difference in the spinning of the pupal case by the larvae of the two species, and Mr. Rohwer writes to me that he believes that the two species "should be retained in different genera for besides a difference in coloring there is a shortening of the petiole in *C. caeruleum* and certain other differences which indicate that it is of a different group." Thus we have convergence of habit of nest-building in three distinct genera.

NIDIFICATION OF *S. CAEMENTARIUM* AND *C. CAERULEUM*

During the sunny days of summer one may see many of these mud-daubers coming to the edges of streams and puddles, critically selecting mud of exactly the right consistency and literally standing on their heads biting out chunks of it and carrying it to some distant shelter. There they fashion it into the familiar cells illustrated in figs. 3, 4, 6, 18. The size and shape of these pellets which they carry may be seen in fig. 13. These were dropped by insects taken at such sources, and are exact size. The smaller ones however are probably incomplete balls dropped by wasps which were interrupted during the gathering. It is generally thought, and all the treatises (excepting the Peckhams'[2]) state that this mud is mixed with the saliva in the mouth of the insect. I do not wish to discredit this statement, for I have no proof to the contrary, but since it is generally made on supposition, I think it would be permissible for us here to suppose also that the amount of saliva used by an insect in a day would be many times the size of the little body producing it, especially when the wasp sometimes constructs a whole cell in an hour and a half, or on other occasions when she is building incessantly, whole days at a time, or reinforcing the nest, as shown by the thick walls in figs. 7, 9 and 10.

In these two species and in *T. albitarsis* as well, the young from eggs deposited in the early fall feed and go through their metamorphosis during the winter and emerge as adults the next

[2] Instincts and Habits of Solitary Wasps, p. 178: "The wasp adds nothing to the mud, depending upon its drying for the necessary firmness, and if by some accident the rain strikes it the whole becomes soft and falls to pieces."

PLATE I

FIG. 1. Pipe-organ nest of *T. albitarsis*. Reduced.
FIG. 2. Same, back view. Reduced.

May or June. Here at St. Louis we have both summer and winter broods, and I have a faint suspicion that those nests which harbor the winter brood of *S. caementarium* and *C. caeruleum* are built more massive than the summer cells. This question is worth investigation to determine whether the wasps are endowed with the instinctive power of apprehending the approaching season. When one sees the enormous thickness of some of the walls (*e.g.*, figs. 7, 9 or 10) in contrast with the thin walls and partitions often found in the summer nests (fig. 20), one is almost tempted to attribute this to something other than individual traits, although we have found an enormous amount of individuality expressed in the work of *S. caementarium*. One finds, for instance, much variation in the careful or slipshod manner in which load after load of mud is applied to the nest. Fig. 4 shows how precisely each mouthful is sometimes applied to form half a ring on the cell, while fig. 8 reveals the careless way in which another mother applied her plaster, without any regard for size, shape or security. I am sure that a nest made as loosely as this would be an easy mark for Hymenopterous parasites of the genus *Melittobia*[3] or even *Anthrenus* larvae when minute, had not this mother made up for her carelessness by thickly daubing mud over the outside of the nest. This photograph shows the details of the contours after the loose reinforcement was carefully scraped off. The nests of *S. caementarium* and *C. caeruleum* usually have additional mud daubed over the outside, no doubt for the purpose of strengthening the structure and increasing its warmth. Some are decorated on top of this with whole pellets stuck here and there over the surface—not flattened or spread as usual (figs. 3, 18). This serves no utilitarian purpose, so far as we can see, and is not generally done, but the very fact that it is sometimes done, shows that individual differences in manipulation exist, and to account for the origin of this difference leads one into fanciful speculation. It certainly seems farfetched to say that some females have developed an aesthetic taste. Better would it be to say that this habit of decorating is a vestige from the time when one or both species, living in milder climate, made a crude nest entirely of small round pellets carelessly stuck together. Later when climatic changes or migration northward occurred,

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[3] They can pass through holes .013-inch in diameter.

those few individuals which builded strong survived, until now
only this vestige remains of what may have been a former habit.

An idea of the amount of effort expended in the construction
of a nest can be gained by examining the cross-sections illustrated
in figs. 7 and 9, and the longitudinal section in fig. 10.

The material used in the nest is usually native clay, gray,
red or various shades of brown, or even black loam. The
Peckhams describe several cells made of white plaster, and I
have several nests taken from the walls of a brick-yard stable
which have some cells made of brick-dust and the remainder
of black mud. Sometimes even the pellets of mud, which make
up a single cell are clearly from different sources.

The favorite nesting-place of these species is the rafters of
barns or sheds, especially when they are high and well out of
reach of intruders. In areas untouched by man the overhanging
rocks and bluffs are favorite nesting-places. One also finds the
mud nests on the back of torn or hanging wall-paper, in the
folds of horse-blankets, old carpet or grain-sacks hanging in
out-buildings, in the sleeves and folds of hanging coats, on old
umbrella ribs, on strands of hay or corn-husks or in small spaces
between the rafters, but in every such case the nest conforms
to its immediate surroundings. It frequently happens that the
nests built in close quarters are very beautiful, since the builder
cannot obliterate her art here by daubing mud promiscuously
all over it. The nests built in folds of cloth or on strands of
hay are usually more asymmetrical than those built flat upon
a board or an overhanging rock, and conform to the folds of
the drapery.

It was once my good fortune to gather a bushel of mud nests
from some freight cars side-tracked in the city. This suggests
a mode of the dissemination of the species not heretofore con-
sidered, and may well be a large factor in their distribution,
since the Peckhams and others think that the wasps do not
usually migrate far from the place of their birth.

On one occasion, when searching for mud nests, I was taken
to a farm-house where the nests were abundant in the upstairs
rooms. The house had not been occupied for the two years
previous to that summer and insects had made themselves at
home in it. The nests were abundant upon the walls and
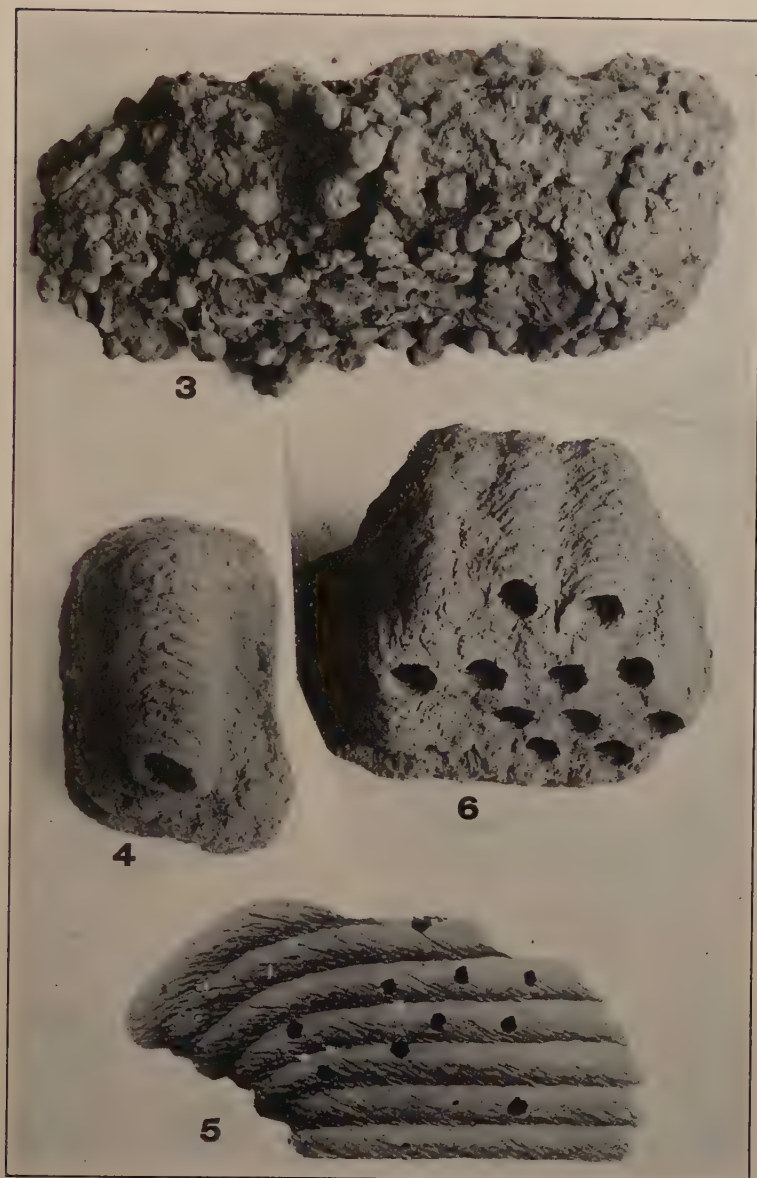window-casings of the upper rooms and many wasps were busily

PLATE II

FIG. 3.   Nests of *S. caementarium* or *C. caeruleum*, with decorations of mud pellets.   Natural size.
FIG. 4.   One-celled nest of mud-dauber.   Natural size.
FIG. 5.   Pipe-organ nest of *T. albitarsis*.   Reduced.
FIG. 6.   A common form of nest of *S. caementarium* or *C. caeruleum*. Natural size.

coming and going.   But when I proceeded to gather them, they all proved to be cells from previous years, and I found that the good new nests were only on the ceiling, just out of reach.   It seems that the wasps built their nests wherever their fancy dictated so long as they were unmolested, but when people occasionally moved about in the room they promptly chose sites higher up, out of the range of disturbance.

The two species of wasps, *Sceliphron caementarium* and *Chalybion caeruleum* make mud nests which are very similar in appearance.   The species of the builder is ascertained with accuracy only by finding the dead pupae or adults in the cells or by noting the species of the adults as they emerge.   Occasionally the nests of both are decorated with pellets.   The only constant distinction which I have been able to discover lies in the difference in the structure of the cocoon; that of *S. caementarium* is smooth, glossy and brittle while that of *C. caeruleum* is the same but covered with a webby mesh.[4]   The occasional occurrence of both species of wasps emerging from one colony of cells does not necessarily mean that an erring mother has deposited her egg in the wrong nest, although it would seem to us almost impossible for a mother to find her own nest among hundreds of others as we sometimes see them massed in the lofts of large barns.   (In our barn, 643 were gathered and about three times as many remained).   The phenomenon is easily explained by the fact that the mud-dauber's nest occasionally occurs on top or along side of the pipe-organ nests, and on several occasions we have found them plastered to paper wasps' nests.   In fact one curiosity which we have is the nest of these two species of mud-dauber and a pipe-organ nest all subjoining a large paper nest.   We can see that probably the mother seldom commits the error of laying her egg in another's nest, but when choosing a site on which to build she sometimes regards the architecture of her sisters the same as the side of a barn.

NIDIFICATION OF *T. ALBITARSIS*

Trypoxylon albitarsis makes the Pipes of Pan, or as they are more frequently called the pipe-organ nests.   Fig. 5 shows the nest as it usually occurs; the short tier is in course of construction.   *T. albitarsis* does not daub the nest all over with

[4] Details in *Psyche*, Vol. XXII, p. 62-63.

mud when it is completed, thereby hiding its artistic architecture, but it, like the other two species, smooths the interior of each cell carefully. The holes at regular intervals in the nest are made by the emerging adults, and the white spots are the hardened chalky substance which the insects emit from their bodies immediately after they emerge. This white substance is emitted by *S. caementarium* and *C. caeruleum* also, but in the form of many minute pellets discharged before emergence.

The larva of *T. albitarsis* spins a very light web about the walls of its cell; just inside this it constructs its cocoon, black very strong and brittle. This it probably makes of the excrement which it clears from its alimentary tract after feeding is completed, and utilizes for a cocoon by throwing it all over itself. This is then kneaded into shape by dextrous movements of the body; it then hardens and makes a very comfortable abode.[5]

These nests are usually built against some flat surface; sometimes the back side is lined with mud, and sometimes the board on which it is plastered serves as a back wall. Here in fig. 2, we have a view from the rear of one such nest built without a back wall, showing cells, partitions, pupal cases, spiders, empty cells and two cells in course of construction. In this nest are three instances of the emerging insect opening its way into an adjoining cell instead of to the outside; if the adult belonging in the latter cell had already emerged, this wasp could leave by its exit, but if not it must certainly die imprisoned, because instinctively the insects can open their way through only one wall.

In contrast to this flat form I have seen about a dozen nests built on hanging corn-husks. Here without a substantial foundation the cells attained a perfectly cylindrical shape, as thick on the back as on the front. They afforded sufficient protection in all respects, however, for they normally brought forth healthy adults.

On only one occasion have I been able closely to observe the details of the building operations of *T. albitarsis* in progress.

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[5] I have tried to observe this process by placing larvae about to pupate in vials. But it seemed they were unable to work on the smooth glass, for they produced only thick ribbons of the black material, but no pupal case.
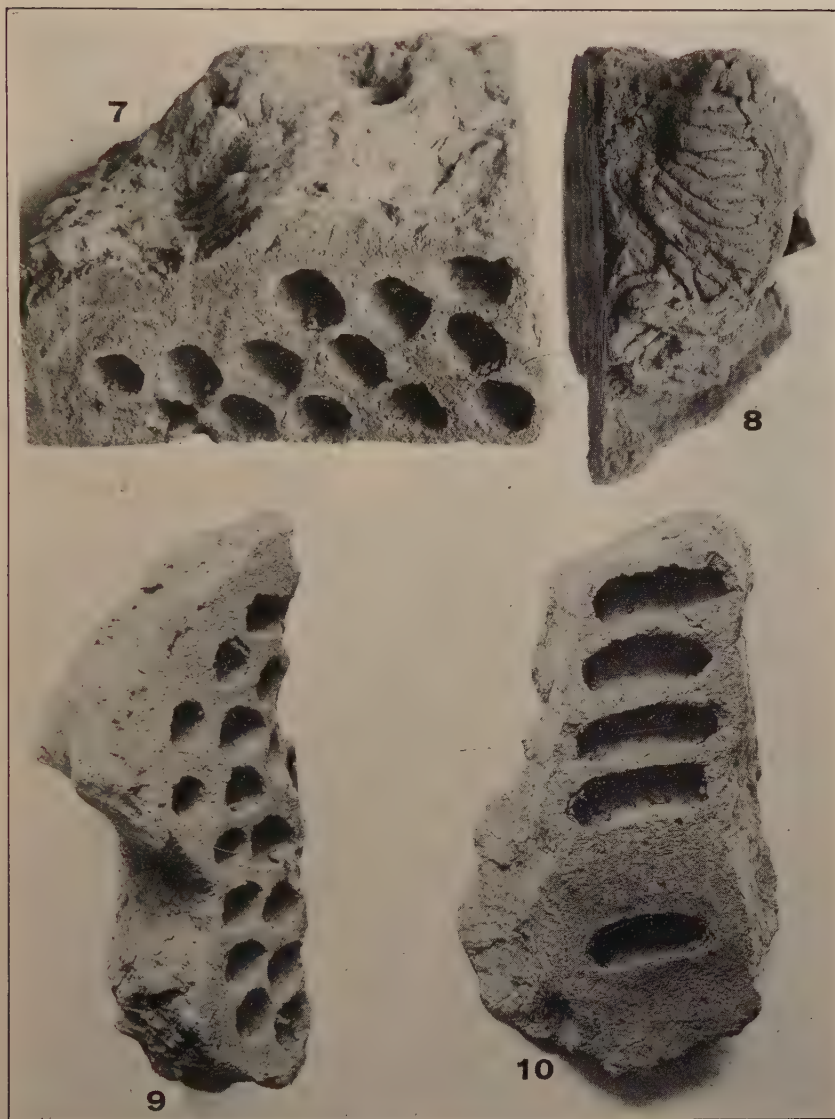
PLATE III

FIG. 7. Cross section of mud-dauber's nest showing the thickness of the walls and the relative position of the cells. Natural size.

FIG. 8. Nest of mud-dauber, showing the details of the architecture after the reenforcing layers of mud had been removed. Natural size.

FIG. 9. Cross section of nest. Slightly reduced.

FIG. 10. Longitudinal section of the mud-dauber's nest, showing the size of the cells and the thickness of the walls. Slightly reduced.

This nest that I was so fortunate to discover in course of construction was in an accessible position so one could easily watch the methods of building. It contained two complete tiers and the third was being added. The wasp returned with a mouthful of mud, but our presence disturbed her and she flew away. Only on her fourth return was she content to settle down to her work without heeding our presence. She would remove the load of mud from her mandibles to her front legs and apply it to the structure in its proper place and then smooth and work it down with her head. Her mud puddle could not have been far off, for she required only from one to three minutes to make the round trip and bring her load of mortar.

As usual, the male remained in the tube that was being constructed while the female brought the mud and continued the building. The male sometimes poked his head out of the cell to meet or greet his spouse, in a way very similar to the habit which we have seen in the smaller species of Trypoxylon (*T. clavatum*). A long pipe was first constructed. This was then filled for a certain distance with spiders and an egg laid with them and a partition put in, making a cell out of this section of the pipe. This process was repeated until the entire pipe was divided into cells, and then a second tier was made beside it. Since most of these nests are built vertically, with the openings downward, one wonders what prevents the spiders falling out while the cell is being filled, the egg laid and the mud applied for the partition. I have wondered whether the male did not in some way perform this office. It was soon necessary for me to leave, so we captured the female and took down the nest. We found the male 'way up in the topmost corner of the unfinished tier. The two older tiers were complete in every way, properly partitioned and sealed, and each cell contained spiders and a young wasp.

·Dr. William H. Ashmead[6] says:"Walsh was the first to record the habits of *Trypoxylon albitarsis*, which usually selects the deserted cells of a mud-dauber (*Pelopoeus*) in which to nidificate, provisioning its cells with spiders. I can confirm this statement of Walsh's from personal observations, as I have not only obtained them from the old cells of *Pelopoeus* but also from those of *Chalybion caeruleum*. I have also bred *T. clavatum* from the same mud-dauber's cell."

[6] The Habits of Aculeate Hymenoptera, II., *Psyche*, Vol. VII. p. 45.

While I can agree with Mr. Ashmead in regard to obtaining adults of *T. clavatum* from the nests of *Pelopoeus* or *Chalybion*, I cannot agree to the statement of both himself and Mr. Walsh that *T. albitarsis* uses the old cells of both these species. Many hundreds of adults have emerged from pipe-organ cells in my possession. In addition I have invariably seen these wasps at work on these nests, so I can hardly think of them as using old cells of other wasps.

One often finds nests parts of which, and especially the middle parts, are two, three or even four tiers high, one built on top of the other, as shown in fig. 1, where two layers exist and a third is being commenced. Whether one mother constructs tier upon tier, or whether a second mother builds her nest on top of the first I do not know. This condition occurs almost too frequently to be attributed to mere accident. Nevertheless the occurrence of nests in this form brings out an interesting point in the instinct of the emerging wasp.

Fabre[7] carried on some experiments with the mason-bee *Chalicodoma muraria*, in which he found that instinctively the animal could bore out of only one earthen covering, and while apparently it had the physical ability to emerge from an extra covering it would rather die in its prison-house than make the extra exertion to escape. But how fares it with these wasps whose mothers or aunts build tier upon tier, making it necessary for the emerging wasp to bite through more than one wall before gaining its freedom? It is interesting here to note that the insects seem to have some faculty of discerning the front side of their cells, just as the larva of the blue wasp or the yellow-legs has the faculty of righting itself about in its cell as it reaches maturity so that it always pupates with its head toward the exit. In *T. albitarsis* nests of only one layer of cells, one seldom sees an error in choosing the proper side for exit. It has been my good fortune to obtain a few nests which were two or more layers deep, and to study their contents to learn whether these wasps did plod faithfully on until they gained their freedom, or gave up at the first defeat. I have little doubt that there is sufficient strength in those mandibles to penetrate several walls, so the question is merely one of instinct. One nest of two layers was placed flat upon a table so that the emerging insects

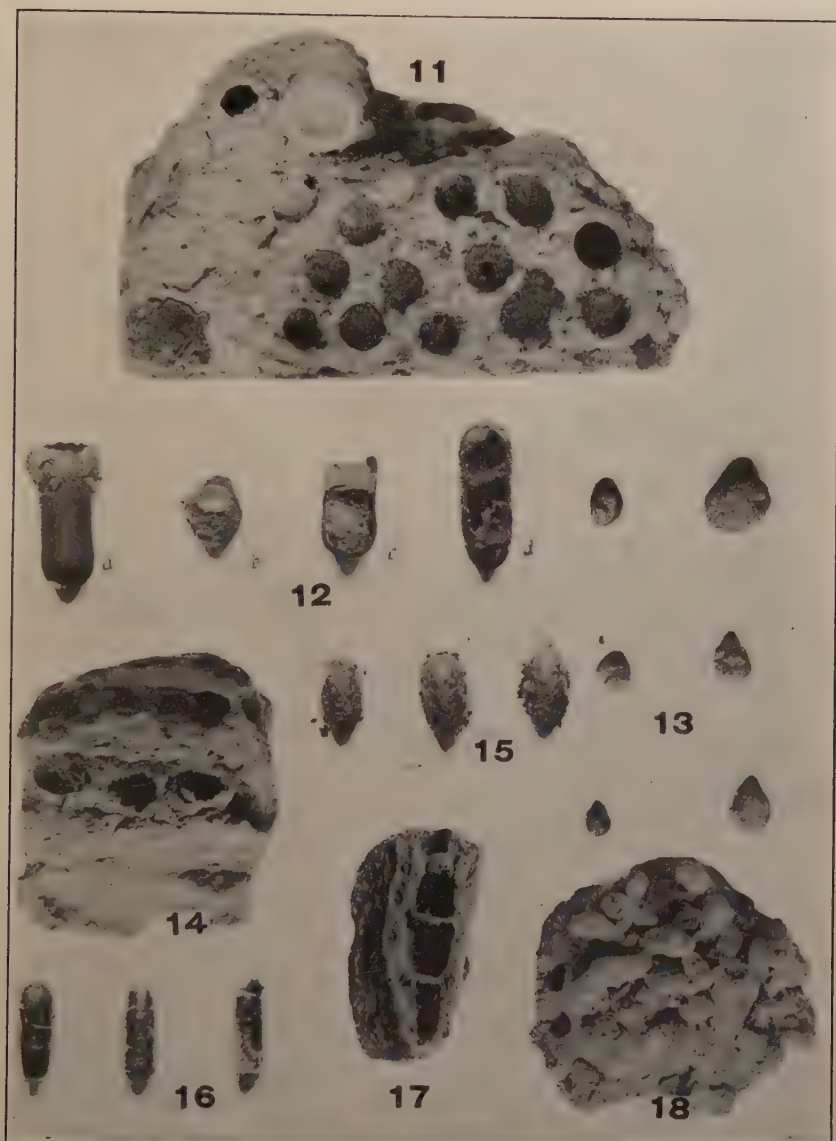[7] The Mason-Bees. Tr. by A. T. De Mattos. Chap. II.

PLATE IV

FIG. 11. A deserted mud-dauber's nest, the cells used by *O. cordata* and the openings resealed with waxy material. Natural size.

FIG. 12. Pupal cocoons of *T. albitarsis* after having been used by *O. cordata; a,* complete pupal case with old opening resealed with wax; *b,* waxy plug removed, showing hole made by emerging *O. cordata; c,* part of cell opened to show pupal case of *O. cordata; d,* cell of *T. albitarsis* opened to show partitions and plug of waxy substance. Natural size.

FIG. 13. Mud balls taken from the mandibles of mud-daubing wasps.

FIG. 14. Longitudinal section of mud-dauber's nest showing the pupal cases of *O. cordata* between the waxy partitions. Natural size.

FIG. 15. Pupal cases of *O. cordata* taken from deserted cells of mud-daubers' nests.

FIG. 16. Pupal cases of *T. clavatum.*

FIG. 17. Old nest of mud-dauber, with two mud partitions, and mud plug in old opening made by *O. lignaria.*

FIG. 18. Nest of mud-dauber, showing decorations of mud pellets. Reduced one-half.

could not gain their freedom by way of the under side, which was partly open; the table merely replaced the board wall upon which it had been built. Fourteen wasps escaped in the normal way from the top layer and the periphery of the lower layer. Seven adults in the central cells could not escape, but each one bored through the wall and entered the adjacent cell, where they were found dead. They followed no special direction in boring out of these lower cells; one had bored through the front wall, and the other borings were equally divided on either side. In one such dungeon three dead prisoners were found, the original inmate of the cell and the neighbor from either side. Had each one of these seven mature insects had the instinctive courage or energy to push on through one more wall, all would have escaped. In another nest we found where this same inability had brought death to one insect, the only one in the nest that was so situated that its exit led into another cell. In a third nest the same was true for two insects. We cannot call this defective instinct, but only simple instinct, for in the insects' normal experience they should have but one wall to penetrate in order to gain their freedom.

One would like to say at least that it is wonderful that the emerging wasp knows how to direct its exit towards the light, but even this is not always the case. I have another record of an eight-celled, one-story nest in which three individuals had bored through the side-wall into their neighbor's cell and died there, instead of breaking through their own roof to freedom. So even this instinct of working out toward the light is sometimes defective.

PARASITES AND LESEES

Often one finds other species occupying the nests or preying upon the wasps at home. Among these are:

Parasites
    Cuckoo-bees, *Trichrysis tridens*[8] Lep. and *T. parvula*[8] Fab.
    Dipteron, *Toxophora americana* Guerin.
    Dipteron, *Spogostylum fur* O. S.
    Dipteron, *Argyromoeba obsoletum* Loew.
    Hymenopteron, *Melittobia*.

[8] Identified by Mr. S. A. Rohwer.

Museum pest, *Anthrenus scrophulariae* L.
Mutillid wasp, *Sphaerophthalma scaeva* Blake.
House-renters
Bees, *Osmia cordata* Robt. and *O. lignaria* Say.
Eumenid wasp, *Ancistrocerus (Stenancistrocerus) fulvipes* Sauss.
Eumenid wasp, *Ancistrocerus camestris* Sauss.
Wasp, *Trypoxylon clavatum* Smith.
Wasp, *Trypoxylon cockerellae* Rohwer.
Wasp, *Pseudagenia mellipes* Say.
Wasp, *Pseudagenia adjuncta* Banks.
Meal-worm larva, *Tenebrio obscurus*.
Small click-beetle.
Lepidopterous pupa, *Apatela*, possibly *radcliffei*.
Mites and spiders.

PARASITES

Perhaps the most destructive of these is *Melittobia*.[9] The parasites enter the mud nests by making holes about .013-inch in diameter, enter the pupal cases in the same way and lay their eggs. The larvae eat the contents of the cell (usually in the prepupal stage), and escape as adults, leaving the cocoon empty. These adults bore holes through the neighboring walls and enter other cells and the life cycle is repeated. That these parasites bore into cells promiscuously is evidenced by the fact that their borings are also found in empty cells. Considering their large broods and the rapidity with which they develop, and their ability when ready to migrate, to bore into the mud cells, it is surprising that even one larva should escape them. They usually attack the organism in the prepupal stage, boring into the cell and then into the pupal case. They do not eat the pupal case, nor do they mutilate it, but leave it intact excepting a few small punctures, and containing a quantity of fine debris—probably their own shedding-skins.

The Dipteron which is directly parasitic upon both *S. caementarium* and *C. caeruleum* is *Argyromoeba obsoletum*, Loew.[10] These flies are by no means rare. The larva is found in the wasp's pupal cocoon; this shows that the parasite attacks the

[9] Identified by Dr. L. O. Howard.
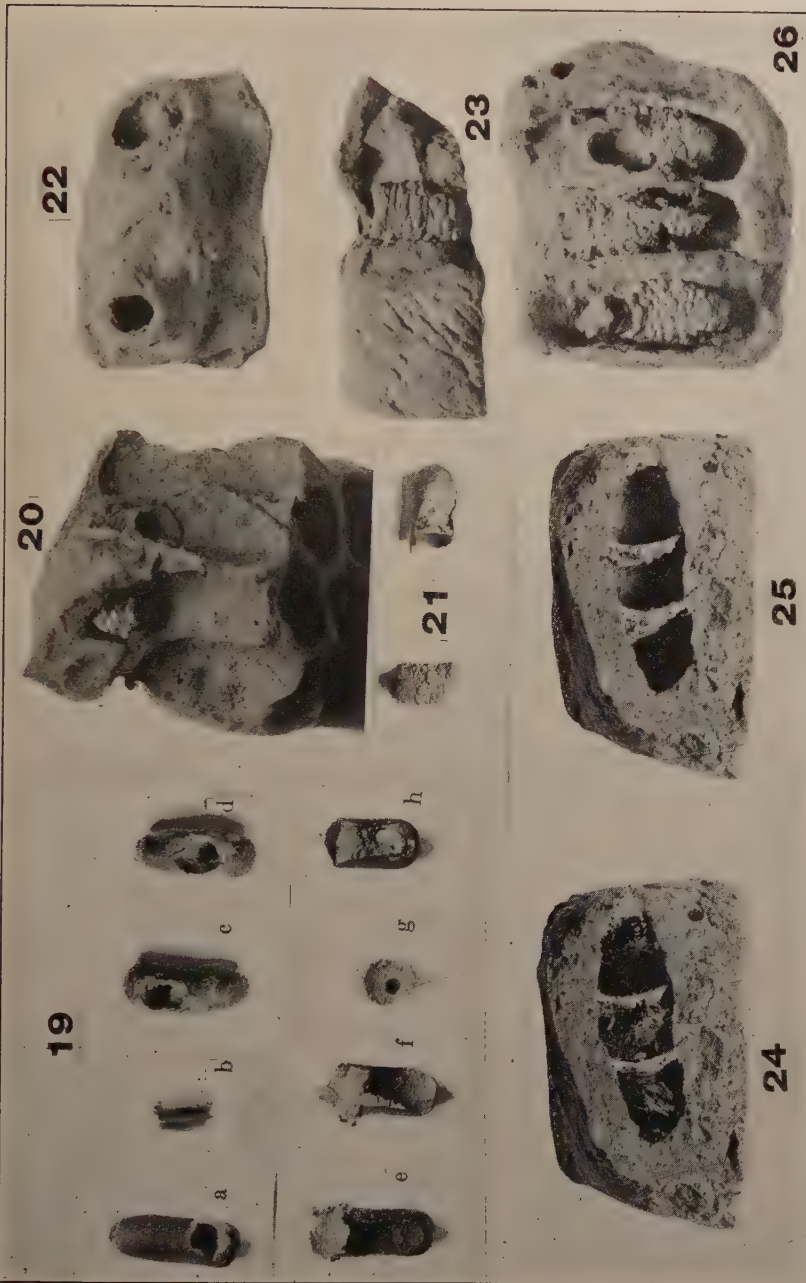[10] Identified by Mr. F. Knab.

PLATE V

FIG. 19. A series of old pupal cases of *T. albitarsis*, used by *T. clavatum* for nidification: *a, c* and *d*, old cocoons with the exits plastered over and the interior lined with mud; *b*, cocoon of *T. clavatum* (one end open); *e, f*, sections of resealed cocoon; *g*, mud plug removed to show hole made by emerging *T. clavatum*; *h*, interior of nest, showing young larva. Natural size.

FIG. 20. Cells of mud-dauber opened to show the two small cells made by *P. adjuncta*. Natural size.

FIG. 21. New cells of *P. adjuncta* built in old pupal cells of *T. albitarsis*. Slightly reduced.

FIG. 22. Mud nest with two hilly protrusions which were cut down to show nest of *P. mellipes*. Natural size.

FIG. 23. Nest of *P. adjuncta* built in part of a nest of *T. albitarsis*. Natural size.

FIG. 24. Old nest of mud-dauber with side-wall removed to show partitions and plug and pupal cases of *T. clavatum*. Natural size.

FIG. 25. Same, with contents of cells removed.

FIG. 26. Cells of *P. adjuncta* in old mud-dauber's nest.

larva just before it reaches its prepupal stage. Even as late as June 1, one often finds upon opening the mud nests, these Diptera larvae which so closely resemble the wasp larvae as to be at first glance deceiving. When the time for emerging arrives this pupa works itself out through the mud wall until it protrudes half way; then the pupal case breaks and liberates the mature, winged insect, the old shedding skin still blocking up the hole made in the mud wall.

Sharp[11] says that the life history of these insects was unknown until Fabre ascertained that another belonging to this genus, *A. trifasciata*, was parasitic upon the mason-bee. This fly, according to Fabre, oviposits by dropping a minute egg on the mass of masonry by which the grubs of the mason-bee are protected. From this egg is hatched a minute larva, which is provided with a horny head and bristles serving as organs of locomotion; thus equipped it explores the surface of the masonry for a long time seeking an entrance. Having penetrated the wall, it undergoes a complete change of form, and without inflicting any perceptible wound upon the pupa it sucks day after day until it has completely emptied its contents. For some months it remains a quiescent larva in the cells of the mason-bee, but in the spring it undergoes another metamorphosis and appears as a pupa, provided with formidable weapons for breaking down the masonry by which it is imprisoned. It strikes against the opposing wall until a gallery of exit is formed; then the pupal skin bursts and the perfect fly emerges leaving the pupal case still fixed in the gallery.

These details describing the European species apply equally accurately to our *A. obsoletum*.

Other Diptera which emerge from the mud-daubers' nests although less frequently, are *Toxophora americana* Guerin[12] and *Spogostylum fur* O. S.[12]

In addition to these two species of Diptera one finds old pupal cases of flies of a smaller species, in the old remains of spiders, etc. in the cells, but I have never yet been able to obtain adults therefrom. There are sometimes from three to a dozen in a single cell.

Birds, while they are neither parasites nor inquilines, should

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[11] *Cambridge Nat. Hist.*, Pt. II, p. 486.
[12] Identified by Mr. F. Knab.

be recorded as an enemy of *T. albitarsis*, which frequently causes heavy losses. It is a simple matter for a bird to peck through the mud walls of the pipe-organ nests and on one occasion a blue jay was actually seen breaking into the nest and to feast upon the larvae therein.

In addition to the above we have found one nest of *T. albitarsis* infested by an Ichneumon fly belonging to the tribe *Ophionini*.

In one collection of *Sceliphron* I found about a dozen cocoons which, when held to the light, revealed an inner cocoon just a little smaller than the mud-wasp's cocoon and of a lighter color. I had found previously that the blue wasp makes an outer webby cocoon over the papery one, but this seemed to be a reversion of that arrangement. At emerging time there issued from these *Sphaerophthalma scaeva* Blake,[13] a handsome black Mutillid parasite with orange abdominal markings. This species emerged from mud-daubers' nests collected in two different localities and years.

We find that the larvae of *Sphaerophthalma scaeva* Blake spin their cocoons within the cocoons of *Pelopoeus*. Since the nests containing both were gathered in December and remained in my living-room all winter, it was impossible for *Sphaerophthalma scava* to parasitize the cocoons of Pelopoeus after they became such, but in all probability the eggs of *S. scaeva* remained dormant until the Pelopoeus larva had finished feeding and spinning, and then it developed, forming its own white cocoon within the brown one of the Pelopoeus. Even this parasite we find parasitized by *Melittobia*.

Some old cells of *T. albitarsis* were infested by mites, probably *Pediculodes ventricosus* Newport, but since there was slight mortality in this lot of material I presumed that the mites had come after the emergence of the wasps to feed upon any old spiders which chanced to be there.

HOUSE-RENTERS

These occupancies other than parasites may be called little more than chance. But the empty cells of the three species of mud-daubers here considered serve a very important function in supplying permanent homes to at least four distinct species

[13] Identified by Mr. S. A. Rohwer.

of Hymenoptera. The bee[14] habitually uses the old cells for her young. She divides them into smaller cells by partitions of a waxy substance, making from one to five rooms out of each original cell. Fig. 14 is a section of two abandoned cells of the mud-dauber, revealing three pupal cases of *Osmia cordata* in each. In the spring one finds these pupal cases (fig. 15) of *O. cordata* in the cells, and occasionally a little pill of bee-bread also. The opening of the old cell is thickly plastered with the same brown, waxy substance (fig. 11.) The mother *Osmia* also uses the old cells of the pipe-organ nests, plastering the opening with a thick layer of wax, or even utilizes the hard cocoon-shells of that species in the same way. Fig. 12 shows these cells in use; *a* is a complete cell with the open end plastered up with wax; *b* is the waxy plug removed showing the hole at one side made by the emerging bee; *c* is part of the cell opened to show the pupal case containing the living organism; *d* is a cell complete, sectioned to show the partitions made of waxy substance, and the plug remains as it was placed over the opening made by the mother *Osmia*.

At what time of the year the *Osmia* fills the cells and oviposits we do not know. The bee is a honey-gatherer, I am sure, and not a parasite in any way. Our individuals kept in confinement fed readily upon sugar water. We conclude, from the occasional presence of the pellet of bee-bread in the cells, that the mother places this food in the partitioned room and lays her egg upon it. When we opened the cells on January 1, 1913, we found the adults in each cocoon completely grown. The bee would crawl about for a time and then when replaced in the nest would gladly creep back into its broken cell. Those which were not replaced were glad to get into any crevice. It seems that during cold weather they remain in their enclosures even though they are fully matured. If a bee is removed before its period of hibernation is completed, it may be replaced in its torn cocoon, or it often goes back into the shell or some other crevice of its own accord and resumes its sleep without ill effect. But when they emerge of their own accord (about the middle of April, if out-of-doors, or in March in the living-room), they have not the ability to rehibernate and soon die unless fed.

These bees have the power of emitting a very pleasant, sweetish

[14] Kindly identified by Mr. J. C. Crawford as *Osmia cordata* Robt.

odor when handled.   This is not acquired from the environment, but seems to be inherent, for when one cuts open a cocoon containing a full-grown insect, the scent greets one.   Whether this scent may be protective we do not know, but we have observed that the dead insects are very attractive to mice.   On one occasion when I left nine *Polistes annularis* and *P. pallides* and seven *Osmia* pinned to a sheet of cork over night, I found the next morning that the *Osmia* were neatly nibbled from the pins and no crumb of wings or legs remained, while the *Polistes* were untouched.   Many of these *O. cordata* pupal cases gave forth Hymenopterous parasites, May 18 to 20, which were identified by Mr. J. C. Crawford as *Monodontomerus montivagus* Ashm.

On September 16, 1915, in an abandoned log-cabin near Eureka, Mo., we took a number of mud nests which at once appeared interesting because the openings of exit had been resealed with mud.   We thought they were the nests of *Trypoxylon clavatum* or possibly a species of Eumenidae, but upon opening the cells at home we found most of the wasps' cells partitioned with mud and containing from two to four little rooms each.   In each compartment I found a pupal case identical in appearance with that of *Osmia cordata*, but *cordata* partitions the old cells with a waxy substance, while in all of these the partitions were of mud.   I cut open several of the cocoons and found a living adult in each.   Here again this species differs from *O. cordata*, since the latter appear as adults in the cocoon in early spring.   These new bees were larger than *cordata* and the characteristic sweetish odor was lacking.   Most of the cells were heavily parasitized by a Hymenopterous species and were in the pupal stage.

The specimens were sent to Mr. J. C. Crawford and identified by him as *Osmia lignaria* Say.   Fig. 17 shows the nest of the mud-dauber, with *O. lignaria's* two mud partitions, and the mud plug in the old opening.

We find a note on this species by Packard (in his Guide to the Study of Insects, p. 139, 1889): "The ♀ of *Osmia lignaria* Say MS., according to Harris' MS. notes was found in the perfect state in cocoons within earthen cells under stones, April 15.   The cell she constructs is one-half inch long, oval cylindrical, and contracted slightly into a sort of neck just before the open-

ing for the exit of the bee. From Mr. James Angus I have received the pellets of pollen, about the size of a pea in which it deposits its egg. The larvae were one-third grown in August.''

This may indicate that the habits of the species have changed within a comparatively short period, and that now she has learned to repair old domiciles instead of building new ones.

Another insect which makes good use of the empty cells of old nests, as well as holes in fence-posts, etc., is the small *Trypoxylon clavatum* Smith.[15] This wasp uses the old cells in much the same way as does *Osmia*, but uses mud instead of wax for partition and sealing material. When this species takes possession of the old cells of *C. caeruleuin* and *S. caementarium*, she uses them without alteration other than the partitions which she throws in, and the closure of mud. Fig. 25 shows these partitions and the mud plug with contents of the cells removed, while fig. 24 shows in situ the pupal cases amid the remnants of spiders' legs. But when she uses the old empty cocoons of *T. albitarsis*, she smoothly lines the old pupal case with fine mud and plasters the opening of the cocoon (which is usually flush with the opening in the mud walls), in the same way. Fig. 19 shows a series of old pupal cases of *T. albitarsis* as used by *T. clavatum*. Figs. *a. c* and *d* show the deserted cocoons of *T. albitarsis* with the exits plastered over or the interior lined with mud. These plugs of mud have in turn been pierced by the emerging *T. clavatum*. Fig. *b* (and also fig. 16) are the cocoons of *T. clavatum*, natural size. The material in this is the same as that of the *T. albitarsis* cocoons, but it is thinner. Since it is itself enclosed in the heavy cocoon of *T. albitarsis* it need not be heavier or stronger. Figs. *e* and *f* show sections of the resealed cocoons; fig. *g* is the mud plug removed from a cell to show the neat hole made by the escaping *T. clavatum*, and fig. *h* shows the interior of a nest of *T. clavatum* where the larva is snug and thriving in the old pupal shell of *T. albitarsis*.

One often finds that the mother *T. clavatum*, before storing the spiders for her young in an old cell has had a thorough house-cleaning, but instead of brushing the rubbish, spiders legs, Anthrenus shedding skins, etc., out through the doorway she has swept them into the corner, as far back as possible, and walled them up with a partition of mud. This is poor

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[15] Kindly identified by Mr. S. A. Rohwer.

economy however, since that room could have been used nicely for another babe. This condition was seen so often that it cannot be attributed to the whim of an occasional individual. In one case we found a living *S. caementarium* prepupa pushed away back and entombed. The mother *caementarium* had failed to seal her cell after laying the egg, and the little *clavatum* treated it as she usually treats rubbish.

In a collection of about a dozen mud-dauber's nests taken in the spring of 1909, one nest gave forth six individuals of *Trypoxylon cockerellae* Rohwer, identified by Mr. Rohwer.

Another member of this group of house-renters is *Pseudagenia adjuncta* Banks. (Identified by Mr. S. A. Rohwer.) This wasp makes complete new cells inside the old cells of mud-daubers' nests (see figs. 20, 23 and 26), and also makes complete cells in the old empty cocoons of *T. albitarsis* (fig. 21).These insects emerged from material gathered at several places near St. Louis, and the adults emerged in late April and early May. I have not observed the insect in the larval stage, but their pupal covering is very thin and papery and of a cream white color.

Likewise a sister species, *Pseudagenia mellipes* Say,[16] shares the benefits of the mud nests. They do not make pretty little cells inside the old mud-daubers' cells, as does *P. adjuncta*, but they emerge from the outside walls of the nest, and I suspect that their nidification occurs in this way. A mother finds the nest of a mud-dauber and with her mandibles digs a small cavity in the outer wall; this she fills with provisions and the egg. Then with the mandibles she removes more earth from the nest and builds up and around her mass until it is completely hidden. If the *Sceliphron* is at work at the time, so that *P. mellipes* can get the wet mud, the work is greatly facilitated. Fig. 22 illustrates the mud-daubers' nests with a portion of the top removed to show the cells from which *P. mellipes* emerged. It may be possible that *P. mellipes* does not dig out her supply of mud from the nest, for in that event she would be obliged to moisten it in some way. But if she brings it from afar I cannot account for the mandible marks which usually are in evidence near by. This species makes a pupal case of soft, white material which is identical with that made by *P. adjuncta*. It appears that these little builders may often be aided in their work by

[16] Also identified by Mr. S. A. Rohwer.

the hostess *Sceliphron* or *Chalybion* who, when reinforcing her nest with layer after layer of mud on the outside, covers the little foreign cell as well and quite obliterates any traces of its presence.

Hartman (Bull. Univ., Texas, No. 65, p. 48-49, 1905) calls *mellipes* a blue insect and describes its habits of nest building. Since Dr. Hartman's *mellipes* differed in color and in habits from the *mellipes* which came from the mud nests of *Pelopoeus*, I again submitted the specimens to Mr. S. A. Rohwer for verification, and he writes: "I have looked over these specimens again and am sure that my determination of them is correct. In most cases Ashmead made the determinations for Mr. Hartman and in many cases Ashmead's determinations cannot be relied upon. We had in the collection of the Museum after it had been arranged by Ashmead three species under the name *mellipes*."

Among other insects which occupy the old mud cells are two wasps belonging to the Eumenidae. From the Kansas material of 1912 several specimens of *Ancistrocerus* (*Stenacistrocerus*) *fulvipes* Sauss,[17] emerged, and in a lot of material from Meramec Highlands in 1911 many *A. camestris* Sauss.[17] appeared. These wasps use the old cells without modification, filling them with caterpillars for their young and then resealing them with mud.

Spiders are often found occupying the old cells, buried deep in a mass of soft web. Often too the larva of the dark meal-worm *Tenebrio obscuris*, is there feeding on the rubbish that remains after the wasp has emerged. Cockroach egg-cases are sometimes found in the cells, and often the pupa of the hairy caterpillar (*Apatela*, possibly *radcliffei*)[18] is found all nestled down in the mass of its own hairs, with the opening of the cell well sealed with the same material.

THE CONTENTS OF THE NESTS
THE KANSAS WINTER BROOD OF 1912

In May, 1912, in an effort to obtain a supply of material for variation studies I shipped to St. Louis from Lake View, Kansas, about 650 of the mud nests of *Sceliphron caementarium* and *Chalybion caeruleum*. All of the nests were gathered in

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[17] Identified by Mr. S. A. Rohwer.
[18] Identified by Dr. H. G. Dyar.

one barn near a stream, and care was taken to select only those which apparently contained pupae. The good nests may be distinguished from the old nests by the openings of egress which the latter contain. This point of distinction may not always be relied upon since occasionally these holes have been replastered with mud or wax by tenants of the old nests, such as *Osmia* bees or small *Trypoxylon* or even Eumenid wasps.

Unfortunately for the variation studies, the most of the cells were either parasitized by *Melittobia* or they had been eliminated in the larval stages by various agencies, so that only a meagre handful of normal adults came from all this collection. Variation studies were defeated, but there arose at the same time the equally important and inviting problem of the rate and causes of this appalling elimination.

So with this large number of nests on hand I took up the task of opening each cell and tabulating its contents. Since the resulting tables are too unwieldy to be practical for publication, it seems best to give the total results of each class of contents of the nests, adding thereto the details of some of the most interesting mother-wasp behavior as revealed by a study of the contents of her cells.

The 643 nests which constituted this lot had a total of 4,397 cells. The number of cells in each nest varied from 1 to 36, as presented in the table below.

Cells to each nest	Frequency	Cells to each nest	Frequency
1	35	15	12
2	73	16	8
3	61	17	7
4	75	18	4
5	72	19	3
6	61	20	6
7	49	21	1
8	37	22	2
9	34	23	2
10	23	24	1
11	26	25	2
12	17	28	1
13	18	30	1
14	11	36	1

The Peckhams[19] found, before the season was over, the number of cells to a nest to be 5 or 6 and the most they ever found was 21.

Out of 4,397 cells I obtained only 172 good adults in June.

[19] Loc. cit., p. 178.

Parasites and lesees

One third of the cells, or to be exact 1,524 contained the parasites *Melittobia* or evidences of their having been there. This parasite was very destructive and was instrumental in wiping out entire families in many instances. Of the 643 nests only 210 were entirely exempt from their attacks, and the smaller nests of 1 to 5 cells were the ones most favored in this exemption. Of the 210 which were quite free from these parasites, 143 or 68 per cent. of them were nests of 1 to 5 cells, while in the entire collection a scant 50 per cent. of the nests were of that size.

In this material we found that the common museum pest, *Anthrenus scrophulariae*, ate not only the dried food as is its custom, but larva and spiders as well. In some cases we found them in the open cells wherefrom the adults had emerged, feeding upon the remains of the pupal case and fragments of spiders' legs, but these were not counted; only those were considered which were found alive in the sealed cells or had matured and left their shedding skins amid the dissected spiders. In that case only were they considered true parasites, destroying living matter. Yet we cannot prove that even here they had destroyed living matter since they may have entered cells which contained no egg or in which the larva was already dead.

Of the 4,397 cells, 171 or 4 per cent. were in this condition, *i. e.*, the cell properly sealed and the contents destroyed by this pest.

Fifty cells gave forth Dipterous parasites, and 5 cells produced cuckoo bees; 54 cells contained the small house-renting *Trypoxylon clavatum*, and 2 cells had been filled with caterpillars and resealed, evidently by an Eumenid wasp; one cell contained an adult chick-beetle which was probably only using the cell for shelter and 3 cells harbored larvae of the dark mealworm, *Tenebico obscuris*, and 1 cell contained a Lipidopterous pupa which later gave forth an adult.

Since the young wasps in the Melittobia infested cells had completely spun their cocoons, it is quite likely that a large per cent of them would have emerged as good adults, had not the parasites killed them. In so far as building and provisioning were concerned the mother wasp was not at fault in these, while

in the case of the remaining cells still to be accounted for she probably was responsible to some extent.

Number of cells provisioned and sealed without the egg

Of the remainder of the cells we find 537, or 12 per cent. of the total, in which the mothers had completed the cell, adequately provisioned it and finally sealed it without laying the egg. This defect of instinct or intelligence is appalling when one thinks of the effort expended in building the nests and the great amount of spider hunting necessary to provision them. We tabulated the number of spiders that came out of 515 of these cells, as follows:

No. of spiders in each cell	Frequency	No. of spiders in each cell	Frequency
1	22	19	4
2	24	20	5
3	32	21	6
4	40	23	2
5	59	24	2
6	56	25	4
7	48	26	5
8	52	27	5
9	23	28	1
10	30	29	2
11	14	30	3
12	9	31	2
13	8	32	1
14	14	33	2
15	8	35	1
16	6	38	1
17	11	42	1
18	11	46	1
		Total 4,637	Average 9

Thus the effort spent in capturing and storing 4,637 spiders (an average of 9 to a cell) was utterly futile because the mother wasp failed to deposit an egg with them. We find the number of such cells in each nest varying from 1 to 17 and occurring with the following frequency.

Eggless cells in each nest	Frequency	Total cells
1	153	153
2	59	118
3	28	84
4	15	60
5	11	55
6	6	36
7	2	14
17	1	17
	275	537

Assuming that each mother is responsible for one nest complete, we find from this tabulation that 275 mothers built and provisioned these 537 cells without laying their eggs therein, and the number of times each mother proved "forgetful" in this respect varied from 1 to 7 times, with the one exceptional case of the largest nest in the whole collection, wherein she failed to oviposit in 17 of them, about one half of the cells which she made. It may be that this exceptional mother was favored with extraordinary longevity and that even after her quota of ova was exhausted her domestic instincts prompted her to go on faithfully building and providing, even though the species would derive no benefit from her labor. The table shows that the greatest number of mothers erred in one or two of their cells, but this is the natural sequel to the fact that a great majority of the nests contain only a few cells. We sought for some correlation between this parental tendency and the number of cells in the nest, but we found none; the large and the small nests were equally likely to suffer from this form of neglect. The phenomenon seems to be largely a matter of individual temperament. Frequently a handsome nest of many cells was faultless in this respect, while sometimes a single cell, the only domestic attempt of the mother, was a dismal failure because she had failed in this vital point of depositing an egg in the otherwise perfect nest. Only in rare cases was the mother forgetful of her egg throughout her work (excepting in single-celled nests); in almost all of the nests we got evidence of fertile eggs in some of the cells. It was for a time thought that probably an infertile egg had been deposited and that this in its shrivelled condition might have been overlooked, so a careful search was always made for any evidence of such an egg, but none was ever found. Since more recently we have watched Mother Sceliphron fill and seal her cells without the egg, we feel reasonably certain in attributing this condition to her forgetfulness or her sterility, and not to infertility. We have not ascertained to what extent the wasp is forgetful of laying the egg, or to what extent this lack of egg-deposition is due to sterility or infertility. If she be sterile or unfertilized, it is even more strange that she should go on making and stocking her cell than that the unfertilized mantis should continue to make her egg-case, for in the mantis the material for the egg-

case comes from her own body, hence the process is physiological, while in the wasp, nidification plus provisioning is psychological in its origin.

Cells that were completed and sealed without provisions or egg

One hundred seventy-six cells, or 4 per cent. of the total number, were properly made but sealed empty. These were made by 132 mothers, who erred in this frequency:

No. unfilled cells in nest	Frequency, or No. mothers	Total No. cells
1	100	100
2	24	48
3	6	18
4	1	4
5	0	0
6	1	6
	132	176

Thus we see that it is an error which is committed occasionally by many wasps (in this population 1 mother out of every 5); but to a large extent by very few. The two cases of 4 and 6 empty cells to a nest were both in large nests, and of the many one-celled nests in the collection only 2 were empty. In other words, a mother frequently leaves one or two cells of her nest empty, but rarely leaves her whole nest, be it large or small, in that condition. In the nest of 36 cells, the largest in the collection, as we cited before, the mother had sealed 17 of the well-filled cells without the egg, but she had failed to provision only one. cell. Some other mothers built large nests without even a single failure in this point.

Number of cells unsealed

We occasionally find cells which have been completed but not sealed; they are sometimes quite empty and sometimes partly filled with spiders. The sight of a deserted cell partly filled with provisions for the young at once suggests another tragedy of the insect world,—a mother wasp who has met her death while out foraging for her brood. But since the mother can meet such a death only once to forever prevent her return to her nest, and since we find some mothers having two to four such cells, we must attribute at least part of these cases to some other causes, such as forgetfulness, etc. There were 126 of

these unsealed cells, or about 3 per cent. of the total number. Of these, 7 were partly filled with spiders. They occurred in the following rate:

No. open cells in each nest	Frequency, or No. nests	Total cells
1	77	77
2	11	22
3	5	15
4	3	12
	96	126

The table above shows that 96 mothers failed to seal their cells, and while most of them (the 77 which failed in one case only) might be attributed to some accident that prevented the mother from returning, yet the 19 other cases prove that part of these failures must be attributed to her carelessness. On two occasions in my experience, adults emerged from these unsealed cells of the summer brood. The closure therefore does not affect the development of the larva, but it probably keeps out parasites.

Insufficient food in the cell

Another occasional fault to be attributed to the forgetfulness or carelessness of the mother wasp is that of laying the egg and closing the cell with a supply of food that is quite insufficient to bring her young to maturity. We find in some cases only enough food to carry the larva through half its period of growth, or even less. When the cells were opened up and dead larvae found, it was noted whether any food remained uneaten in the cell. If the larva was dead and part of the food was untouched, its death was attributed to unknown causes. If however a half-grown or stunted larva was found dead in the cell with no food, its death was attributed to starvation, due to the mother's failure to supply it with sufficient food.

Only 46 cells, or 1 per cent. of all, were found in this condition, and 35 mothers were responsible for this mischief; 29 of these mothers had one such cell each in their nests, and these nests were distributed among the large as well as the small nests (2 to 26 cells). Four cases of two such cells in a nest were among small nests. The mother that erred in this way three times had a 7-celled nest, and last of all one wasp with a 25-celled nest was woefully deficient six times.

One sees that experience counts for little, that there is no relation 'twixt large nests and learning to fill them properly.

Spiders that remained uneaten in the cell

In contrast to the condition mentioned above, there were some cells wherein the insect was past the feeding stage and in the prepupal, pupal or adult condition, and some spiders still remained uneaten. When this occurred, they were counted to see to what extent the mother may give a superfluity of food.

There were 135 such cells, in contrast to the 176 cells which the mothers had sealed stark empty, and 46 in which she had sealed up the egg with insufficient food. So it seems that the mother wasp is more likely to err by giving her child too little food than by offering too much. The following figures show the number of spiders that remained in each cell after the larva had spun its cocoon.

No. spiders	Frequency	No. spiders	Frequency
1	14	8	9
2	31	9	1
3	30	10	4
4	10	11	0
5	16	12	2
6	12	13	0
7	3	14	2
		15	1

The number of spiders that remained untouched varied from 1 to 15, the greatest frequency occurring between 1 and 6 spiders.

Mortality in the larval stage

Here we consider the mortality of the organism in the larval stage of growth, due to causes other than starvation. We know this because in every case some uneaten food remained in the cell. The 245 cells, near 6 per cent. of the whole mass, were distributed as follows:

No. such cells in a nest	Frequency or No. nests	Total No. cells
1	95	95
2	29	58
3	9	27
4	4	16
5	2	10
6	3	18
7	3	21
	145	245

Mortality in the prepupal stage

Those eggs which are deposited in late August and September winter over as prepupae in the nest. In a comparatively short time the larvae consume their food and grow to full size, and long before cold weather sets in they have spun their cocoons about themselves and there they remain inactive, not transforming into pupae until spring (about May). In this condition they pass through the coldest part of the winter, and a part of the mortality among prepupae may be attributed to the cold.

When the cells are opened and dead prepupae are found, they are of two kinds, (a) those which are dead, but are yet white in color, which shows that they have died more recently than (b) those which are of a decayed-looking, brown color, showing their death to have been more remote, and hence having occurred earlier in the season, when they had not experienced much cold. In this collection we found 415 belonging to class a and 629 to class b. This shows that the mortality was greater in the earlier and milder period than during the colder season. Of course other external factors may have been responsible for the life or death of the insects, such as the thickness of the mud walls, etc.

The mortality at this stage including both early and late deaths was 1,044, or about one fourth of the cells. There may have been some inherent weakness in whole families, but this will be discussed under mortality in individual families.

Mortality in the pupal stage

After the insects have survived the winter in the prepupal stage they transform into pupae. Here in the more advanced stage of the insect's life the mortality was comparatively small, 110 cells, or 2 per cent. of the total. But even this number is large when one considers that the insect is past most of its frailties and difficulties, feeding, spinning and transforming; why should these have died for no apparent cause at this vigorous stage? This subject too will be considered again in the probable inherent weakness of certain families.

Mortality in the adult stage before emergence

Here we have a rather perplexing form of mortality. The insects had transformed properly into adults, had wings, legs,

antennae and mouth-parts, and yet were dead in their cells, some of them still in their cocoons; others were out of the cocoon but had died before biting their way out of the cell or even while doing so. In this stage we find the mortality to be 130, or 3 per cent of the total.

Elimination within individual families

We have found that a certain per cent. of the cells that are built cannot possibly bring forth adults. In some cases the defect is the fault of the mother in not having properly filled the cell, or having forgotten to lay the egg, etc. In other cases no adults can be expected to emerge, but through no fault of the mother, as for instance, where the young are destroyed by parasites. However, there is in each nest or colony a portion of the cells which contain all the rudiments for producing a new generation, but the organism may or may not have the inherent vitality to press on to the completion of its development. For want of a better name we shall be obliged to refer to these throughout the succeeding paragraphs as the potentially productive cells or the potentially emergable young wasps.

There were in this collection 1,701 such cells, or 39 per cent. of all built by these mothers. Even among these which were apparently unhampered by any obstacles to their growth and were supplied with all things required for their development to adulthood, we find heavy elimination in different stages. This loss of life is due largely, I presume, to inherent weakness, or if not inherent weakness, to what might be called the inability of some individuals to resist extreme conditions which only the most vigorous individuals can survive. It is a startling discovery that in this population, barely one out of ten of even these apparently perfectly equipped young ever lived to see the light of day.

When we examine certain nests we find the potentially good organisms eliminated in some colonies in many different stages of their development; in other nests it is clear that these un-molested and promising young have all dropped off at the same stage of their development, although not at the same time of the calendar, from which we may infer that their death cannot be attributed to some environmental catastrophe, but to some cause within themselves.

I assume that each nest is built and filled by only one mother, and in this assumption I feel fairly confident. So when we find all of the young of one mother (as in some nests we do), either emerging as adults or dying in the stage just preceding emergence, then I say this mother has endowed her offspring with better constitution to do battle with adversities during its postembryonic development than the mother whose entire progeny has died in early larvahood.[20]

The greatest elimination occurred in the prepupal stage. Of course we must bear in mind that in the winter brood this stage covers a long period when the organism rests in this condition during the winter, not transforming into a pupa until early spring; hence we must expect a proportionately greater mortality. In some cases we find whole families dying in this stage of their development; in other colonies the individuals live through this critical period only to drop off later, for reasons unexplained, and still others all survive to adulthood. In some cases they never reach even full growth in the larval stage. But the point that we would emphasize here is that the young not only die, but a certain considerable proportion of them die with precision and system. When we find all of the population of a nest arriving at an advanced stage, or in another all dying at an early stage of their development, are we not right in suspecting that the good tendency or the bad tendency "runs in the family" or may be heritable?

In going into a study of elimination in this group, we should bear in mind that the mud-daubing wasps offer us material which is peculiarly simplified for such a study. Many species during their development from egg to adult would have to face the chance of elimination in open competition with their fellow-beings and enemies, and can only reach adulthood by surviving climatic conditions in the open and also by exercising enough energy and art to procure their own food during tender youth as well as avoiding being food for others. But with these wasps the case is very different. Not an iota of exertion or responsibility is required of them until they arrive at adulthood. In this part of the population, where the young are constantly

[20] Variable environment can scarcely have been a factor here, since all of the nests here considered were taken from the rafters of the same barn, in equally sheltered positions.

sheltered from the weather and enemies, and their food is at hand for them when they arrive, and with the two fierce struggles removed (hunting for food and being hunted), one would expect little or no loss of life, and it certainly would appear that, aside from inherent tendencies, all had exactly equal chances of survival.

Hence we must admit that Natural Selection is vigorously at work here, eliminating weaklings while the vigorous survive, even in this secluded life where the individuals do not in any way come into the open struggle for existence. It is precisely this elimination in the potentially viable young in single families that we shall now take up.

It is difficult when so many elements are involved to get any tangible proof that inherent characteristics of families have anything to do with the mortality or viability of these young. We may approach it however by calculating what the death-rate would be in each of the five stages or combinations of stages[21] if the elimination followed only chance. The entire formula for all of the possible combinations of the five stages is so long that we shall only take from it what we want to compare with the actual occurrences in the preceding tables. It is obviously necessary that all of the nests must have at least five good cells to justly compare them with the distribution of five chances, so we use in the following comparison only the nests of that size or greater. Of these, we had 120.

Now if no factor but mere chance controlled the distribution of the fatalities, then there would be only one chance in 3,125 of all five of the young in a nest meeting death in any one stage, while in fact we find this actually occurring at a much higher rate, e. g., all died in the prepupal stage in 22 of the 120 large nests, or at the rate of 572± in 3,125. Other comparisons are as follows:

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[21] We must make due allowance for the fact that in this calculation we have assumed that the chances of death are equal in the five stages, while in fact some stages are obviously of longer duration or more trying than others.

	Proportion in 3,125		Fact, in 120	
	Proportion of			
	Chance	actual occurrence	Chance	Fact
All larvae.............................	1	26	.04	1
All prepupae.........................	1	572	.04	22
All pupae............................	1	52	.04	2
All dead adults.......................	1	0	.04	0
All emerged adults....................	1	78	.04	3
Dead adults + emerged...............	30	104	1.15	4
Dead adults + pupae.................	30	52	1.15	2
Larvae + prepupae...................	30	494	1.15	19
Prepupae + pupae...................	30	234	1.15	9
One or more of each.................	120	52	4.61	2
One or more in 4 of the 5.............	1200	494	46.15	19

Of course, by the time we have selected only the nests of five good cells or more, the numbers are so small that the probable errors are absurdly high, yet to my mind the evidence gives sufficient and conclusive proof of the point we are seeking, *viz.*, the existence of family tendencies of survivability, entirely apart from environment. In the above we see all or nearly all of the family dying in the same stage or in two consecutive stages at a far higher rate than chance would produce, while in the last two groups of miscellaneous distribution of mortality, where the chances run vastly higher, the actual occurrence drops proportionately lower.

So in this heavy elimination which goes on we may justly lay a considerable part of the responsibility upon the parents. In turn they themselves may not have been properly endowed, and we can only regard with the kindliest respect those mothers whose offspring we see surviving in large numbers. There are a few family records which we cannot pass by without marvelling at their perfection, while at present we can only vaguely say that the best of mothers endowed their offspring with the characteristics that make for survival, and the poor mothers put their young here minus these survivabilities, and they went to the wall in spite of the luxurious ease of their young lives.

We regret being unable to go further into the details of this fascinating study of inherent tendencies in individual families, but these numbers scarcely warrant further analysis. The problem is pregnant with biological suggestions for anyone who can obtain the material in unlimited quantities, and it lends itself admirably to mathematical analysis for anyone who might care to work it up by such methods.

Summary of the Kansas winter brood

The 4,397 cocoons from our 643 nests fall into the following classes:

	No.	Per cent
Cells giving good adults	172	4
Cells sealed and filled with spiders, but no egg	537	12
Cells sealed entirely empty	176	4
Cells unsealed with few spiders and no egg	7	..
Cells unsealed and empty	119	3
Cells having dead larva and insufficient food	46	1
Cells having dead larvae and sufficient food	245	6
Cells having dead prepupae	1044	24
Cells having dead pupae	110	2
Cells having dead adults	130	3
Cells infested by *Melittobia*	1524	34
Cells infested by *Anthrenus*	171	4
Cells containing cuckoo bees, Diptera, *Trypoxylon*, etc	116	3
	4397	100

Thus the elimination in this lot is so high that we are almost forced to believe that this is in some way an abnormal population. It is clear that the species could not endure under this rate of elimination indefinitely—in fact, at this rate the species would be exterminated in four years. We know that the abundance of any species varies from year to year, according to its environment. We may have taken this sample after the population had just passed through especial adversity, such as a severe winter, a raid of parasites, etc.

There is a possibility also that a fault exists which we could not avoid in the collection of the material, and that a few old nests of a former year or brood were mixed with these. While collecting them we were careful to keep only those nests which had no openings of egress or other evidence of their being old; hence it is clear that unbroken old nests wherein the young had died in an early stage or had been riddled by parasites, would be indistinguishable from those of the present brood. The number of old nests cannot be large, however, because most of the nests gave positive evidence of newness in at least a part of their cells.

THE ST. LOUIS WINTER BROOD OF 1913

In the early spring of 1913, 31 nests containing 171 cells of these two species of mud-daubers were taken at Meramec Highlands, near St. Louis, Mo.

The number of cells varied from 1 to 17 to the nest. The adults emerged the following June. The contents of these 171 cells were as follows:

	No.	Per cent
Cells producing good adults..............................	47	27
Cells filled and sealed without egg......................	18	10
Cells sealed empty..	16	10
Cells unsealed, containing few spiders...................	0	..
Cells unsealed and empty.................................	8	5
Cells containing dead larvae and insufficient food.........	3	2
Cells containing dead larvae and sufficient food...........	1	..
Cells containing dead prepupae..........................	29	17
Cells containing dead pupae.............................	3	2
Cells containing dead adults.............................	4	2
Cells parasitized by *Melittobia*.......................	37	22
Cells parasitized by *Anthrenus*........................	1	..
Cells parasitized by Diptera............................	4	2
	171	99+

We shall here compare this lot only briefly with the preceding winter brood from a different locality, and go into fuller comparison with the summer brood to follow.

There is a conspicuous difference in the proportion of adults emerging. Here 27 per cent. of the cells built produced adults, yet even this is not enough to maintain the population. In this lot the nests contained on an average only 5.5 cells; if they had averaged 9 cells to each mother, as the Kansas material did, then the population would just maintain itself under the rate of elimination shown here. The principal differences in the mortality in the groups is found in the larval and prepupal stages and the parasitized cells. The lower percentage of loss here just balances the gain in the increase in the productiveness of the population.

THE ST. LOUIS SUMMER BROOD

The second brood, or first summer brood, emerged from nests built in June and July of the same summer. The 110 nests which furnish the data of this group were gathered during July at Meramec Highlands, St. Louis, Mo. Owing to the earliness of the season, the greatest number of cells in a nest was 8, and the total number of cells examined in this lot was 438. Their contents were as follows:

	No.	Per cent
Cells producing good adults............................	225	51
Cells sealed with spiders but no egg...................	27	6
Cells sealed empty......................................	28	6
Cells unsealed, with few spiders.......................	1	..
Cells unsealed and empty...............................	16	4
Cells containing dead larvae and insufficient food........	3	1
Cells containing dead larvae and sufficient food...........	9	2
Cells containing dead prepupae.........................	42	10
Cells containing dead pupae............................	13	.3
Cells containing dead adults...........................	8	2
Cells parasitized by *Melittobia*.........................	32	7
Cells parasitized by *Anthrenus*.........................	32	7
Cells containing Diptera or *Trypoxylon clavatum*..........	2	..
	438	99+

It is at once apparent that this summer brood was far more prosperous than the winter broods just considered. We are not at all surprised at this when we consider that their whole development was accomplished during a brief period of favorable conditions. They did not have to endure the rigors of winter and the increased chances of casualty incident to the prolonged period of dormancy.

Let us take up briefly a comparison of the causes of failure in the two broods. In the first entry in the tables, *viz.*, the per cent. of the cells which brought forth good living adults we are startled by 51 per cent. of the summer cells being fruitful against only 4 per cent. and 27 per cent. of the winter crops of cells. In an attempt to account for this we shall compare the other classes, to locate the discrepancy. The per cent. of cells properly made and provisioned, but sealed without an egg, is noticeably larger in the winter broods. Since we found in a previous chapter (see p. 47) that the large nests were no more likely than the small ones to be affected thus, we cannot attribute this difference to the smaller summer nests. It might be, however—this is mere conjecture—that a part at least of the winter nests are constructed by the wasps late in the fall, in their feeble old age, and hence a larger proportion of these eggless cells might occur than in the nests built by the vigorous young mothers early in the season. In other words, this kind of failure might be attributed to some real physical inability of the parent, and not to mere carelessness or faulty instinct.

The next five groups are surprisingly similar, down to the number of larvae which died of starvation, which is 1 or 2 per cent. in all broods. Hence we have every reason to believe

that the mothers' habits or instincts relative to nest-building are fairly constant at all times.

In the group of those which died as larvae amid plenty of food, the death-rate runs higher among the winter brood than in the summer brood. At present I see nothing to account for this unless it be that the cold of winter caught a few which had not yet pupated. However, the per cent. is so small in both cases that the difference might be little more than mere chance.

Those which died as prepupae show even a more marked difference, 24 and 17 per cent. against 10 per cent. Now this is the stage in the insects' development which is greatly prolonged in the winter brood to cover the period of dormancy. Also it is the stage wherein the insects pass through the winter cold and may succumb to it. Both of these factors cause the probability of fatality to increase. But when we turn to the pupal and adult stages, which are very similar in duration and conditions in the two broods, we again find the per cents of mortality practically identical.

The greatest difference of all occurs in the proportion of young wasps killed by parasites (or riddled by them after their death from other causes. *Melittobia* had infested 34 per cent. of the Kansas winter brood, and 22 per cent. of the Meramec Highlands lot, while it had reached only 7 per cent of the summer lot. This is probably due to the prolonged period of exposure to chance of attack during the prepupal stage. *Anthrenus* was somewhat more destructive in the summer brood.

Hence, we see that practically the whole difference in the mortality in the two broods occurs in these three groups which we have pointed out, where the mothers late in the fall failed to deposit eggs in the cells, where the young died in the prolonged prepupal stage, and where they were the victims of parasites

But this does not end the problems of regeneration of these species. Some large factor is as yet undiscovered. Let us first look at the winter crop of nests. If we may assume that each nest stands for one mother, then the 643 females gave to the next spring's population only 172 new wasps. Now supposing one half of these were males, then the task of keeping up the stock is left to 86 females. If they in turn build nests and

produce a summer brood in the same proportions as the summer
brood which we have just analyzed, then these 86 females will
in turn produce 172 new young wasps, males and females.   Hence
the summer brood, by far the more thrifty of the two, can
barely reproduce its population without any increase, and that
only if we allow nothing at all for the death of the adults as
they work in the fields, or for the utter destruction of the nests
by man, etc.   So if this rate of elimination were typical, (even
without, as just mentioned, any elimination in free adult life),
the species in this locality could continue for only four years,
by which time it would be exterminated.   Or if we take the
Meramec Highlands winter population as typical, this exter-
mination would go on as surely, although more slowly.   But
we know that these species have continued abundant in these
regions for a great number of years.   So how is the population
maintained?   Is there still another brood or two each year,
besides those two here analyzed?[22]   If so, they must be very
prolific to replenish the fast diminishing stock.   Some expla-
nation must still be advanced to account for the presence and
continuance of this large population here.   Of course it may be
that for some reason our samples are not typical of what regularly
occurs in the population.   Every care was taken to avoid any
injury or abnormal exposure of the material at any time.   Since
I know of no work similar to this, we can only look to future
investigations for comparative data to determine whether these
were in all ways typical samples.   Of course the two popu-
lations came from different localities, but they are so near and
so similar in climatic conditions that I can scarcely believe
that the differences of locality would cause such different results.

THE CONTENTS OF THE PIPE-ORGANS, THE NESTS OF
TRYPOXYLON ALBITARSIS

The pipe-organ nests are not so abundant in the vicinity
of St. Louis as are the clustered mud cells.   This chapter deals
with these nests gathered in the early springs of 1912, 1913
and 1914.   The data for the three years represent 1,282 cells.
Since many of the nests were broken in transporting them home,
we shall study each season's lot separately in considering the
contents, but for the data of the number of cells in each nest,

[22] Ent. News.   Vol. XXVI, p. 469-471.

we shall select the complete ones from the entire series.   These 43 nests were of the following sizes:

No. of cells to nest	Frequency	No. of cells to nest	Frequency
42	1	13	1
27	1	12	4
26	1	11	3
25	2	10	2
22	1	9	2
19	1	8	1
18	3	7	2
17	1	6	2
16	3	5	3
15	3	4	2
14	2	3	2

This series shows no pronounced mode.   The nests were gathered in the winter, hence we have reason to believe that they were as nearly complete as were available.   It may be, however, that the population of mother wasps which constructed these nests included old wasps which may have worked all summer on the nest, as well as newly hatched ones which had only a short time in which to build a few cells before being overtaken by winter.

The contents of all these cells were recorded.   In addition, the broken nests were likewise examined and tabulated; these made 709 more cells.   The table below is a summary of the data of these three annual collections, comprising 1,282 cells.

Year	Total No. of cells	No. of cells giving good adults	No. of cells sealed with food no egg	No. of cells sealed-empty	No. of cells unsealed with food	No. of cells unsealed and empty	No. of cells having dead larvae with insufficient food	No. of cells having dead larvae with sufficient food	No. of cells with dead prepupae	No. of cells with dead pupae	No. of cells with dead adults	Parasitized by Melittobia	Parasitized by Anthrenus	Cells having other parasites	Per cent of cells that gave good adults
1912	552	447	51	15	..	..	2	18	1	1	6	..	2	4, O 5, D	81%
1913	203	112	15	11	1	2	2	1	12	10	1	17	12	7, D	55%
1914	527	413	60	1	..	..	..	1	24	1	6	9	..	7, O 5, D	79%
Total	1282	972	126	27	1	2	4	20	37	12	13	26	14	28	76%

How cheering it is to find that 972 of these, or 76 per cent. gave forth good adults in the spring after wintering in the cells. In 126 cases (10 per cent.) did the mothers err in filling the cell or fail to oviposit; 27 cells (2 per cent.) were sealed empty, but in some of these cases the sealing partition was so placed that the room was so small that a growing larva could not possibly have had room to develop anyway. We have never yet noticed *Sceliphron* committing this blunder of constructing her cells too small to permit the full development of her young. There was only one cell that was unsealed containing a few spiders; this case may well have been due to the sudden death of the mother. In only 4 cases can death in the larval stage be attributed to insufficient food, while 20 others died in the larval stage despite the fact that much food remained untouched in their respective cells.

The deaths in the prepupal, pupal and adult stages were 37, 12 and 13 respectively, lower per cents than occurred in the other species.

These insects were preyed upon by some of the parasites of *Chalybion* and *Sceliphron* but not to so great an extent; 26 cells were parasitized by *Melittobia* and 14 showed that the *Anthrenus* beetle had played havoc; 28 cells were divided between a Dipterous parasite and an Ichneumon belonging to the tribe Ophionini, indicated in the table by "D" and "O."

Thus elimination in all the stages of development is far less in *T. albitarsis* than in the other species.

So here we have three species so similar in morphology that we cannot discern any differences which would give one or the other the least advantage in the struggle for existence. Likewise their life history, their habits of living and their habits of nesting are so similar that it would appear to us that they have equal chances of surviving. And yet there exists this remarkable difference in the survivability of these species, and even more strange it is that the species which has the fewest numbers in this vicinity is the one which thrives far better than the others. Had the variation studies, for which the material was first intended, been carried to a conclusion, we *might* thereby have located some tendencies which would account for the comparative vigor or weakness in these species, but I think it more than likely that in pursuing variation problems

purely, we would have been sidetracked on some feature of the insect's anatomy which is entirely irrelevant to its ability to work out its own salvation. But if now the variation studies could be taken up in the light of the preceding paragraphs, they might lead us to profitable problems of the existence or nonexistence of correlation between variation and elimination, or in other words, to add one more word to the hypothesis of selective elimination.

THE IMPORTANCE OF PRIMACY IN THE LEARNING OF A PIG

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During the summer of 1911 the writer performed some experiments on an eight-week old pig. While there are many obvious imperfections in the experiments the records emphasize an important aspect in the learning process, namely, the tendency of the first of a series of habits to possess a relatively high persistency.

The apparatus was very simple. When not fed the pig was shut in a pen X from which a door Y led into a lane L 23 feet in length. Near the end of the lane was an opening O which led into the general pen P whose measurements were 10 x 12 feet. Five feet from either side of P was a board K 7 inches high, parallel to the lane. This board was so high that the pig could not naturally see over it. In either of the corners of P farthest from O and equally distant from it was placed a food receptacle which could be transferred from one corner (A) to the other corner (B).
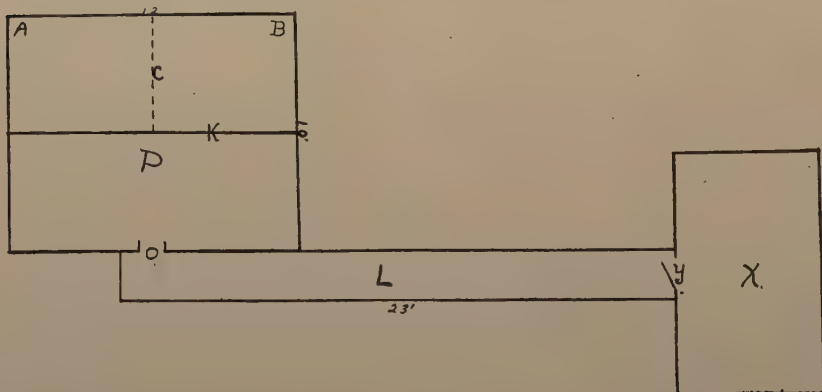
In the first instance the pig was released at Y and found his way into A where he soon found the food, morning noon, and

evening of the first day. On the second and third feedings he ran directly to A without hesitancy. Each time, as soon as his meal had ended, he was shut up in X.

The food always was put into the receptacle before the pig was released so that he could not see it until he had crossed K.

Second Day

Fed every 2 hours. Food was put regularly into B.

First feeding. When released the pig ran directly to A as on the first day, not finding food he rambled about much disturbed for several minutes. Finally he ran a little farther to the right than before and found the food at B.

Second feeding. The same procedure as in the first, but in about half the time.

Third feeding. He ran as before, directly into A; then immediately to B.

Fourth feeding. Same as third feeding, but in less time. Each time when he had consumed the food at B he would return to A looking for food there. He was never fed to satiety.

Fifth feeding. Before he was released, a partition C, 8 inches high was placed mid-way between the two feeding places. He entered the A side directly then, with almost no hesitancy, jumped over the partition toward B. There he was so disturbed he did not get the food at B but jumped out over K. After a number of quick false movements he jumped back over K to B and ate the food. There was no more running to A after the food was eaten.

Sixth feeding. Jumped directly into the A side, came out over K and with no false moves turned to the right and jumped over K to B.

Seventh feeding. Same as sixth.

Third Day (Still fed at B)

First feeding. He made a bee-line from O to A, back over K, to the right, and to B over K.

Second feeding. He made a bee-line for A but only raised his head and looked over K, paused a few moments, turned and jumped over K near partition, into B side.

Third, fourth, and fifth feedings. Made a bee-line from O to B.

Fourth Day

He was fed only three times, morning, noon and evening, when he always made a bee-line from O to B.

Fifth Day (Feeding place changed to A)

First feeding. He made a bee-line for B, searched for food with restless movements, jumped out over K, then scarcely moving to left at all, jumped over K to A.

Second feeding. He jumped into B, then with practically no pause, over partition to A.

Third feeding. Started for B side, but looked over, paused, then into A. In going to B side, however, his pathway diverged a little toward the partition, a decided modification of old pathway from O to B side.

Fourth feeding. Same as third but divergence greater, i. e., nearer partition.

Fifth feeding. He ran directly toward A side but very close to partition, paused without looking over, and jumped directly into A side.

Sixth and Seventh feedings. Made a bee-line to A.

Sixth Day (Feeding place changed to B)

First feeding. He made a bee-line to A but jumped over partition quickly to B, as if planned, with no appreciable pause. Now another board of 6 inches was added to partition C, making it 14 inches high.

Second feeding. He made a bee-line to A but this time he came out of A over K, then to right into B side.

Third and fourth feedings. Same as second.

Fifth feeding. In bee-line to A side but near partition looked over, then turned and jumped into B.

Sixth feeding. He ran directly into B side, but near partition. No pause.

Seventh Day (Morning. Feeding place changed to A)

First feeding. He ran in a bee-line into B out over K, and into A.

Second feeding. He ran directly to B side near partition looked over and very quickly jumped into A.

Third feeding. Bee-line to A.

Seventh Day (Afternoon. Feeding place changed to B)

First feeding. He ran directly to A looked over cautiously, then jumped into B.

Second feeding. He ran to B side, near partition, looked over and jumped into B side.

Third feeding. Directly over B side near partition.

Fourth and fifth feeding. Same as third.

Sixth and Seventh feedings. Bee-line from O to B.

Eighth Day (Morning. Feeding place changed to A)

First feeding. In bee-line toward B, looked over K, and put fore feet over K, then drew back and jumped into A.

Second, third, fourth, and fifth feedings. Bee-line from O to A.

Eighth Day (Afternoon. Feeding place changed to B)

First feeding. Bee-line for A, quickly out and into B.

Second feeding. Directly to A side, looked over, then into B.

Third feeding. Same as second.

Fourth feeding. Directly to B side near partition and into B.

Fifth feeding. Bee-line from O into B.

The following figures show the number of times the pig was fed A and B respectively and the number of right and wrong trips to each.

	No. times fed in A	Wrong trips to A	No. times fed in B	Wrong trips to B
First Day	3	0	0	0
Second Day	0	7	7	0
Third Day	0	2	5	0
Fourth Day	0	0	3	0
Fifth Day	7	0	0	4
Sixth Day	0	5	6	0
Seventh Day (Morning)	3	0	0	2
Seventh Day (Afternoon)	0	1	7	0
Eighth Day (Morning)	5	0	0	1
Eighth Day (Afternoon)	0	3	5	0
	18	18	33	7

While in all, the pig was fed 18 times in A and 33 times in B, he wrongly entered B (i. e. when the food was placed in A), 7 times and wrongly entered A 18 times or, 33.3 per cent. and 54.5 per cent of the responses, respectively, were wrong.

It took only the first feeding to establish a direct pathway from O to A, but after two repetitions of this trip it took ten

trials before the subject learned to go directly from O to B. After going directly to B three successive times it took only five trials to learn to go directly from O to A again. To make the next transition of the pathway (from OA to OB) it took six trials. Hence, while primacy tends to persist throughout it decreases somewhat with time.

The modification in the learning is worthy of note. The excited, random movements so obvious in the earlier new situations which successively appeared with the alternation of feeding places, decreased as the experiment progressed. On the other hand the responses to the later situations were characterized by hesitancy and by attempts to use the eyes to help determine, before jumping over the board K, which was the right way to go. To illustrate; on the twelfth feeding which was the second feeding of the third day, after having gone from A to B eight successive times, he paused at K at a point on a straight pathway to A from O, raised his head high enough to look over K, then turned and jumped over K near the partition into the B side. Likewise at the third and fourth feeding of the fifth day, after making two wrong trips to B, he paused at K, looked over and turned and jumped into A. His pathway, moreover, instead of being in a straight line from O to B diverged a little toward the partition, and on the succeeding trip diverged still more, so that the next time he jumped directly into the A side but near the partition. At the fifth feeding of this same day, instead of looking over K, he ran to it in line with A, paused, and jumped into the A side. These gradually shifting pathways seem to indicate the resultant of two antagonistic impulses. It must be remembered here that although the subject often took the wrong pathway from O, eventually he always found the food; but in finding the food after first entering the wrong side the subject never went back to O for a new start, but sought the food by the shortest way he could find from where he was. No doubt the transitions from one pathway to another, from O, could have been completed with fewer errors if the corrections could have been made from O. Even then, theoretically, there would have been some tendency to make the wrong trip again and to return to O rather than to go to the food directly. In any event, the mere recency of the appeal of the stimulus where it once was, does not so much account for the tendency to con-

tinue to take the wrong pathway as the persistency of the impulse to go from O by the pathway that last was successful from O to the food. It is interesting to note that the pathway taken at the first feeding of each morning was always the same as the pathway taken last on the previous day.

An example from the writer's experience of an attempt to break a certain habit of forgetting may help explain the principle involved. On two successive evenings he forgot to extinguish the gas light in the cellar after he had made the fire. On the third evening as he closed the cellar door behind him, on entering the kitchen he remembered that he had left the light burning and he at once returned to extinguish it. For about a score of evenings he went through exactly the same process of forgetting and correcting. Just as soon as the thought of the light suggested itself when the fires had been made, the proper reaction to the light was elicited. Again, it is not so much the attraction of a stimulus that determines a certain reaction as it is the precedence and strength of that reaction to that stimulus.

The results of this experiment are significant in showing the tremendous force and persistency of the first of a series of habits. Of course humans are not pigs but fundamentally the methods of learning for pigs and people are about the same. Therefore, these records suggest the gravity of the "first impression," and emphasize the importance of correct reactions at the outset in any kind of learning.

It is to be regretted that the time for each reaction was not recorded and that some device was not provided whereby the exact part of K over which the pig jumped in his search for the food could be determined, and that the experiment was not continued for a much longer time. While these results are not at all conclusive they probably suffice to warrant further study along the same lines on small children as well as on animals.

THE MARRIAGE-FLIGHT OF A BULL-DOG ANT
(*MYRMECIA SANGUINEA* F. SMITH)

WILLIAM MORTON WHEELER

During a recent visit to Australia I had an opportunity to study in the field the habits of a number of species of the large ants popularly known as "bull-dog ants," belonging to the very primitive genus *Myrmecia*. This genus comprises some sixty described species, subspecies and varieties, all confined to Australia and the island of New Caledonia. They bear about the same relation to the more specialized and more modern ants that the Marsupials of Australia bear to the placental mammals of other continents. Many of the species are among the largest of ants, several of them are beautifully colored and sculptured, and all of them sting or both sting and bite severely. In his latest work on the Ponerinae in the "Genera Insectorum" Emery divides the genus *Myrmecia* into three subgenera, *Myrmecia* sens. str., *Pristomyrmecia* and *Promyrmecia*. I have found that the species of these three groups differ greatly in nesting and other habits. A detailed account of my observations will be published later in connection with taxonomic descriptions of the various forms. Here my remarks will be mainly confined to one of the largest and most aggressive species, *Myrmecia sanguinea* F. Smith, an ant which must be widely distributed in Australia, since it has been recorded from Queensland, New South Wales, South and Western Australia and Tasmania. I found it very abundant at Salisbury Court, near Uralla in northern New South Wales, where, through the courtesy of the government entomologist, Mr. W. W. Froggatt, I was able to spend a few days at a laboratory recently established for the study of the blow-flies that have acquired the unfortunate habit of injuring living sheep.

In the open forest surrounding the laboratory there are many large nests of *sanguinea*, mounds of earth of a more or less conical shape, varying from three to five feet in diameter at the base and one to two feet in height. The surfaces of these

mounds are covered with a thin layer of bits of charred wood, dead leaves, twigs and pebbles collected by the ants. The entrance to the nest is a rather small hole, scarcely more than half or three quarters of an inch in diameter and usually situated on one of the slopes near but not at the summit.

Each nest contains about 200 to 500 workers. These are subopaque, rich brownish red in color, with the gaster shining black, and vary considerably in size, from 12 to 28 mm. The females measure 26 to 28 mm., the males 18 to 20 mm. The smallest workers, not exceeding 12 to 15 mm. in length, function as door-keepers and are usually found stationed just within the nest-entrance, with their long, scissor-like mandibles directed outward. When the nest is disturbed these small workers are the first to sally forth, followed by others of the same or medium size, and it is only somewhat later that the huge and formidable individuals, measuring 25 to 28 mm. advance to the attack with wide open jaws and threatening sting. This behavior is the reverse of that observed in other ants (e. g. in species of *Camponotus*, *Colobopsis*, *Atta*, *Pheidole*, etc.), the major workers or soldiers of which act as door-keepers and are among the first to rush to the defence of the colony. Unlike the puny, small-eyed ants of our northern latitudes, the bull-dogs can clearly discern objects at a distance of several feet with their great, prominent, abundantly facetted eyes. They lose no time in running about in all directions hunting for the intruder, but with ferocious unanimity make directly for him. The extraordinary tenacity with which they hold on with their mandibles to any moving object that comes in their path is, of course, responsible for their popular name, but no one has been able to suggest a polite epithet that will do justice to the virulence of their sting.

At the time of my visit to Salisbury Court, during the last week of November, there were no winged males or females in the nests, though there were plenty of larvae and a small number of worker pupae. This is rather surprising because the sexual forms of most of the ants of New South Wales are to be found in the nests during late October and early November. Mr. Froggatt expressed the opinion that the males and females of the various species of *Myrmecia* do not mature till January. This opinion has been confirmed in a letter recently received, in which he describes a remarkable marriage flight of *sanguinea*

in a locality very near the one in which I studied the nests. Fully to appreciate his description, the reader must bear in mind what I have said about the size of the females of this ant. They, of course, have powerful stings, like the workers, though the males are stingless and have feeble mandibles. Mr. Froggatt's account runs as follows:

"On January 30th, after some very hot, stormy weather, while I was at Chevy Chase, near Armidale, N. S. W., I crossed the paddock and climbed to the top of Mt. Roul, an isolated, flat-topped, basaltic hill, which rises about 300 feet above the surrounding open, cleared country. The summit, about half an acre in extent, is covered with low "black-thorn" bushes (*Busaria spinifera*). I saw no signs of bull-dog ant nests till I reached the summit. Then I was enveloped in a regular cloud of the great winged ants. They were out in thousands and thousands, resting on the rocks and grass. The air was full of them, but they were chiefly flying in great numbers about the bushes where the males were copulating with the females. As soon as a male (and there were apparently hundreds of males to every female) captured a female on a bush, other males surrounded the couple till there was a struggling mass of ants forming a ball as big as one's fist. Then something seemed to give way, the ball would fall to the ground and the ants would scatter. As many as half a dozen of these balls would keep forming on every little bush and this went on throughout the morning. I was a bit frightened at first but the ants took no notice of me, as the males were all so eager in their endeavors to seize the females."

Except for the great size of the participants, this nuptial flight presents an exact picture of occasional flights of some of our common Myrmicine ants, especially of *Myrmica scabrinodis* Nyl. That such enormous swarms of *Myrmecia* as the one described must be of rare occurrence, is evident from the statement of such a keen observer as Mr. Froggatt that he has "never before seen more than a dozen winged bull-dog ants of any species together." I find, however, a brief description by Tepper[1] of what must have been a very similar scene. He describes a nuptial flight of one of the large species of *Myrmecia*

[1] Observations about the Habits of Some South Australian Ants. *Trans. & Proc. Roy. Soc. S. Austr.*, **5**, 1882, pp. 24-26, 106-107.

(probably *sanguinea* or *pyriformis*), early in April in South Australia, as "rather a formidable affair, owing to many hundreds of the large creatures (the female above an inch in length while alive) flitting about one's head, all armed with a sting about a quarter of an inch in length, while the shrubs near the nest were covered with scores of pairs and single ones."

The observations of Tepper and Froggatt prove conclusively that the species of the Ponerine genus *Myrmecia* celebrate a regular marriage flight like all the ants of the other taxonomic subfamilies, except the species with wingless males or females, and that these flights occur during January in northern New South Wales or a few months later in the more southern and colder portions of Australia. This season corresponds, of course, to our autumn months, which are likewise the nuptial season of some of our species of *Lasius* (*L. claviger* Roger, *brevicornis* Emery, etc.) We may also infer from the accounts of the two Australian observers that each female *Myrmecia*, after fecundation, loses her wings in the same manner as other ants, except certain parasitic species, enters the ground and establishes a small colony without the assistance of workers of her own species. I am able to show that this is actually the case. On September 19, 1914, I found under a stone in one of the deep sandstone canyons near Katoomba, in the Blue Mts. of New South Wales, a fine deälated female of *Myrmecia tricolor* Mayr occupying a little cavity in the soil and engaged in caring for about a dozen small larvae. This little incipient colony was very similar to those just established by our common carpenter ants (*Camponotus pennsylvanicus* DeGeer and *noveboracensis* Fitch) under the bark of old logs. That the most primitive of existing ants should found their colonies in precisely the same manner as the most highly specialized species, is not without interest.

JEAN-HENRI FABRE

William Morton Wheeler

Through the death of Jean-Henri Fabre on October 11th, 1915, the world has lost its greatest entomologist, a man who combined in an extraordinary degree the gifts of a virile and penetrating observer and those of a literary artist of high distinction. During the greater portion of a life of poverty, extending over a period of 92 years, he ceaselessly devoted himself to an intensive study of insect behavior and to the recording of his observations in such fascinating language that Victor Hugo styled him the " Homer of the insects."

Like the life of his countryman Latreille, who preceded him as the " prince of entomologists," Fabre's life was uneventful. His biography has been written by a sympathetic admirer, C. V. Legros, and rendered into English by another admirer, Bernard Miall, but from many passages scattered through Fabre's great work, the " Souvenirs Entomologiques " it is possible to glean an even more illuminating and intimate knowledge of his powerful individuality and of his methods of working and thinking. He was born of humble peasant parents on December 22nd, 1823, in the hamlet of Saint Léon, in the part of the Provence known as the Haute-Rouergue. Through diligent application to the classics, physics, chemistry and mathematics in the rather mediaeval schools of his day he prepared himself to become a teacher. At 19 he entered on this profession in the College of Carpentras and in 1850 accepted a position as professor in the lycée of Ajaccio, Corsica, at a salary of £72. Here he met the naturalist Moquin-Tandon, who seems to have had an important influence in determining his career as a biological investigator. Even as a boy, however, Fabre had been greatly interested in insects, so that Moquin-Tandon probably only helped to reveal to him his innate aptitude for observation and experimentation. He realized that he had a genius for observing small animals, and from that time forth,

like Socrates, he implicitly obeyed the voice of his daemon almost to the hour of his death. Falling ill with malaria at Ajaccio he was compelled to return to France, and in 1853 was appointed assistant professor of physics at the lycée of Avignon. This post he held for nearly 20 years (till 1871), without advancement and with a salary not exceeding £64! During this period he made some of his most important observations. The written accounts of his work, contributed to the " Annales des Sciences Naturelles " include a study of the habits of the solitary wasp *Cerceris* and of the cause of the long conservation of the beetles on which it feeds (1855), notes on the life-history of *Cerceris*, *Bembex* and *Sitaris* (1856), followed by his classic memoir on the hypermetamorphosis and habits of *Sitaris* (1858) and studies on the rôle of adipose tissue in the urinary secretion of insects (1862).

In 1871 he left the lycèe of Avignon to devote the remainder of his life to the study of instinct in insects. He moved to Sérignan, a hamlet near Orange, not far from Avignon. Here he lived henceforth and worked as a hermit and here he died, in a little cottage on a plot of ground called the " harmas," a beautiful description of which is given in the opening chapter of the second series of " Souvenirs." ¹ During the early years of his residence at Sérignan he was compelled to devote much time to writing text-books on natural history subjects for the purpose of keeping the wolf from the door. It will probably be found that these little books were the forerunners of the modern " nature books." He also continued to contribute scientific articles to the " Annales des Sciences." Two of these, on the habits and parthenogenesis of some bees of the genus *Halictus* (1880) and one on the repartition of the sexes in the Hymenoptera (1884) are of unusual interest. But the great work accomplished at Sérignan is embodied in the ten volumes of the " Souvenirs." Anything like an adequate review of this monumental work would require much time and labor. Only the entomologist who has endeavored to work out complicated insect life-histories will fully appreciate Fabre's powers as an observer and will not be greatly surprised to learn that during the course of years he wore a groove in the stone floor of his

¹Translated by A. T. de Mattos in the "Life of the Fly," Dodd, Mead & Co. 1913.

laboratory by walking around his table. The complete eluci-
dation of some of the life-histories, like that of the sacred scara-
baeus, required observations extending over a period of nearly
forty years.

The newspapers and magazines have made us familiar with
the romance of the closing years of Fabre's life. Mistral, the
Provençal poet, Maeterlinck and Rostand are said to have dis-
covered Fabre and to have called the attention of the world
to his destitute condition. According to a well-known French
magazine, "In 1910 he was revealed to the people; a group
of litterateurs and savants conceived the idea of offering this
modest, almost unknown man a plaque to perpetuate the memory
of his work. Two years later his ninetieth birthday was cele-
brated by a ceremony at which the Institut was represented,
and somewhat later the President of the Republic paid him a
visit." "Why," asks Le Gros at the close of his account of
the celebration of 1910, "at this jubilee of the greatest of ento-
mologists, was not a single appointed representative of ento-
mology present?" And he goes on to say: "The fact is that
the majority of those who 'amid the living seek only for corpses',
according to the expression of Bacon, unwilling to see in
Fabre anything more than an imaginative writer, and being
themselves incapable of understanding the beautiful and of dis-
tinguishing it in the true, reproached him, perhaps with more
jealousy than conviction, with having introduced literature into
the domains of science." This is an unfair statement of the
case. Fabre has long been known to naturalists and especially
to entomologists and many of them, from Darwin to the Peck-
hams and Forel have referred to his work in terms of the greatest
admiration. It is only the litterati and general public who have
just discovered Fabre, and it is not difficult to account for this
belated appreciation. Insects are so peculiarly organized and
offer to the casual observer so few points of contact with the
general trend of human interests that even the magic style of
a Fabre failed to elicit a widespread desire to know about their
activities. But when a great writer like Maeterlinck announced
that, "Henri Fabre is one of the greatest and purest glories in
the present possession of the civilized world, one of the most
erudite naturalists and the most marvellous poet in a modern
and truly legitimate sense of the word," and added that Fabre

was one of the profoundest admirations of his life, people who had never devoted five minutes of their lives to studying an insect, began to sit up and take notice.

Whenever there is complaint of the neglect of a genius by the world, it is well to scrutinize the behavior of the genius. If we do this in Fabre's case we shall have little difficulty in accounting for the neglect from which he suffered, both on the part of the general public and the scientific fraternity. Fabre and his publisher are undoubtedly responsible for much of the popular neglect. The title of the great work, "Souvenirs Entomologiques," is inept, to say the least; the ten volumes were unattractively printed and inadequately illustrated and the arrangement of the articles in the series might have been much better. All rights of translation, even of extracts, were, moreover, rigidly withheld till very recently. When Fabre became more generally known these faults were corrected by the publication of selected essays in more pleasing volumes and under more appropriate titles, such as "La Vie des Insectes" and "Moeurs des Insectes," an arrangement which has been followed in the English translations now displayed in all our bookstores.

The reserved and unsympathetic attitude of entomologists towards Fabre was very largely due to the fact that he was a crotchety and opinionated recluse, who seems never to have made the slightest attempt to enter into friendly personal or epistolary relations with other entomologists, who never mentioned and probably never read the work of his contemporaries, who lost no opportunity of holding up to ridicule some of the most important entomological studies, such as insect taxonomy, and who repeated investigations that had been made by others, without intimating and evidently without knowing that such investigations had long been known to the entomological world. He failed to realize that entomologists are more human than the objects of their studies and that "wer Liebe ernten will, muss Liebe säen." It is not surprising, therefore that there was no afflux of entomologists to Sérignan to celebrate his jubilee. While their presence might have been commendable, we can hardly blame them, under the circumstances, for staying at home.

Another reason for the attitude of entomologists towards

Fabre is to be found in his peculiar views concerning instinct, views that were prevalent enough in the early part of the nineteenth century but are singularly foreign to the psychology and theoretical biology of the present day. He not only declined to accept the doctrine of evolution but vigorously attacked it in more than one of his essays, although many of his criticisms so far overshoot the mark that one reads them with amazement. It must be remembered, of course, that Fabre was nearly 36 years old when the " Origin of Species " appeared. He was not, therefore, like the naturalists of the present generation, suckled, so to speak, at the breasts of evolutionary doctrine, and his life-long lack of contact with biological speculation kept him from viewing the phenomena of instinct from a genetic standpoint. But even in his chosen field, the study of instinct, he confined himself to a comparatively circumscribed group of phenomena. He worked only on a series of insects selected from his immediate environment and for certain peculiar reasons took little interest in the social species, (ants, social bees and wasps) which are, nevertheless, abundant in southern France. His studies on these forms are limited to an essay on the amazon ant (*Polyergus rufescens*) and a few essays on wasps (*Vespa vulgaris*). He seems to have borne a grudge against the ants because they so often entered his breeding cages and killed the insects with which he was experimenting. There were also other and more weighty reasons for this neglect of the very insects which naturally suggest a genetic interpretation of instinct. Fabre believed that instinct manifests itself in its purest form in the solitary species. He was, moreover, greatly impressed by its fixity and mechanical aspect, and his rigid training in physics, chemistry and mathematics and his keen analytical ability probably biased him in favor of views which have grown more and more repugnant to modern biologists. He had a strong tendency to schematize his observations and to ignore the variability of instinct. This tendency has been pointed out by several observers and is most clearly marked in his classic work on the solitary wasps.

Although Fabre suffered in the estimation of many biologists on account of the theoretical views which he elaborated and very stubbornly upheld through the course of a long life in voluntary isolation from the great current of biological thought,

we are bound to confess that in some very important matters his vision was clearer than that of his contemporaries. He alone realized the great significance of the study of animal behavior at a time when other biologists were absorbed in purely morphological work. No better proof of this statement can be given than the concluding paragraphs of the first essay in the second series of the " Souvenirs " published in 1882. I quote from de Mattos' translation (pp. 26 and 27): " Laboratories are being founded, at great expense, on our Atlantic and Mediterranean coasts, where people cut up small sea-animals, of but meagre interest to us; they spend a fortune on powerful microscopes, delicate dissecting instruments, engines of capture, boats, fishing crews, aquariums, to find out how the yolk of an Annelid's egg is constructed, a question whereof I have never yet been able to grasp the full importance; and they scorn the little land-animal, which lives in constant touch with us, which provides universal psychology with documents of inestimable value, which too often threatens the public wealth by destroying our crops. When shall we have an entomological laboratory for the study not of the dead insect, steeped in alcohol, but of the living insect; a laboratory having for its object the instinct, the habits, the manner of living, the work, the struggles, the propagation of that little world, with which agriculture and philosophy have most seriously to reckon ?

" To know thoroughly the history of the destroyer of our vines might perhaps be more important than to know how this or that nerve-fibre of a Cirriped ends; to establish by experiment the line of demarcation between intellect and instinct; to prove, by comparing facts in the zoological progression, whether human reason be an irreducible faculty or not; all this ought surely to take precedence of the number of joints in a Crustacean's antenna. These enormous questions would need an army of workers, and we have not one. The fashion is all for the Mollusc and the Zoophytes. The depths of the sea are explored with many drag-nets; the soil which we tread is consistently disregarded. While waiting for the fashion to change, I open my harmas laboratory of living entomology; and this laboratory shall not cost the ratepayers a farthing."

Not only was Fabre the first to realize the full importance of a scientific study of animal behavior but he was the first

consistently to apply the experimental method to the investigation of the animal mind. The " Souvenirs " abound in accounts of experiments, performed for the purpose of elucidating the nature of instinct, not the less illuminating and conclusive because they were carried out with crude, home-made apparatus. It is as instructive as it is humiliating to read his results and to reflect on the mountains of complicated apparatus in our modern laboratories and the ridiculous mice in the form of results which only too frequently issue from the travail of " research."

Another valuable service of Fabre consisted in his calling attention to the fact that the applications of zoology to human welfare must be based on an accurate knowledge of animal behavior. This has been tacitly assumed by economic entomologists, but neither they nor the modern behaviorists have sufficiently emphasized the fact that we cannot hope to control animal depredations or to compel animals to contribute to our well-being and wealth without an exhaustive knowledge of such apparently remote phenomena as the animal sensations, reactions and instincts. Fabre is quite explicit in this matter. Though he lived as a recluse from the scientific world, he remained in intimate contact with the life of the Provençal peasant and had no doubts concerning the important bearing of his own work on such a fundamental industry as agriculture.